AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3017, 54 pp., 33 figures, 8 tables June 28, 1991

Herpetological Results of the 1990 Venezuelan Expedition to the Summit of Cerro Guaiquinima, with New Tepui Reptiles

MAUREEN A. DONNELLY[1] AND CHARLES W. MYERS[2]

ABSTRACT

Cerro Guaiquinima is an immense sandstone table mountain in the pantepui region of eastern Venezuela. The authors collected 15 species of amphibians and reptiles during 12 days in the dry season (February) at elevations of 1030–1150 m above sea level. One species of lizard (*Plica lumaria*, n. sp.) and two of snakes (*Liophis torrenicola*, n. sp., *Philodryas cordata*, n. sp.) were discovered in the botanically curious *Stegolepis-Clusia* "savanna" and appear to be endemic to this mountain.

Predominantly tepui species found on Guaiquinima that are more broadly distributed in Venezuela include a frog, *Hyla benitezi*, and a lizard, *Neusticurus racenisi*.

The remaining 10 species are primarily lowland animals widely distributed in Amazonia and/or Guayana. These include four frogs (*Hyla minuta, Osteocephalus taurinus, Leptodactylus longirostris, L. rugosus*), five lizards (*Ameiva ameiva, Anolis chrysolepis planiceps, A. fuscoauratus, Neusticurus* sp., cf. *rudis, Tropidurus hispidus*), and a vine snake (*Imantodes lentiferus*) not previously recorded from Venezuela.

Despite its large area, Cerro Guaiquinima is among the lowest tepuis in average height. Although a tepui element is preserved in the herpetofauna, there is a predominance of widely distributed lowland species. This finding agrees with Steyermark and Dunsterville (1980), who commented on the strong lowland floral element on the summit of this mountain.

RESUMEN

El Cerro Guaiquinima es una inmensa mesa de piedra arenisca en la región de pantepui de Venezuela oriental. Una colección de 15 especies de anfibios y reptiles fue hecha por los autores dur-

[1] Boeschenstein Research Fellow, Department of Herpetology and Ichthyology, American Museum of Natural History.

[2] Curator, Department of Herpetology and Ichthyology, American Museum of Natural History.

ISSN 0003-0082 / Price $5.30

ante 12 días en la temporada seca (febrero) en elevaciones de 1030–1150 m sobre el nivel del mar. Una especie de lagarto (*Plica lumaria*, n. sp.) y dos especies de culebras (*Liophis torrenicola*, n. sp., *Philodryas cordata*, n. sp.) fueron descubiertas en la curiosa "sabana" de *Stegolepis-Clusia* y pueden ser endémicas a esta montaña.

Especies de los tepuis más ampliamente distribuidas en Venezuela, encontradas en Guaiquinima, incluyen una rana, *Hyla benitezi*, y un lagarto, *Neusticurus racenisi*.

Las otras 10 especies son principalmente animales de tierra caliente que son ampliamente distribuidos en Amazonia o Guayana. Éstos incluyen cuatro ranas (*Hyla minuta*, *Osteocephalus taurinus*, *Leptodactylus longirostris*, *L. rugosus*), cinco lagartos (*Ameiva ameiva*, *Anolis chrysolepis planiceps*, *A. fuscoauratus*, *Neusticurus* sp., cf. *rudis*, *Tropidurus hispidus*) y una culebra "bejuca" (*Imantodes lentiferus*) que no se habían registrado anteriormente de Venezuela. A pesar de su área grande, Cerro Guaiquinima es de los más bajos tepuis en altura promedio. Aunque algunos elementos de los tepuis se preservan en la herpetofauna, hay una predominio de especies ampliamente distribuidas en las tierras bajas. Este hallazgo concuerda con Steyermark y Dunsterville (1980), quienes comentaron sobre el fuerte elemento florístico de las tierras bajas en la cima de esta montaña.

INTRODUCTION

The table mountains or *tepuis* of the Guayana Shield are mostly sandstone vestiges of the Roraima Formation and are clustered primarily in southeastern and southern Venezuela—-south and east of the Río Orinoco. Among the largest of these is Cerro Guaiquinima (about 5°46′N, 63°36′W) in the state of Bolívar. Expeditions from the Colección Ornitológica Phelps provided data on the bird fauna of Cerro Guaiquinima (e.g., Zimmer and Phelps, 1946; Mayr and Phelps, 1967) and the flora was more recently treated by Steyermark and Dunsterville (1980). Mayr and Phelps (1967: 280) estimated that Guaiquinima covered 440 km^2 (330 km^2 summit area + 110 km^2 talus area). However, according to Steyermark and Dunsterville (1980: 287), satellite imagery shows it to be nearly four times larger than that; these authors estimated a total area of 1600 km^2, including a summit area in excess of 1000 km^2. Steyermark and Dunsterville gave an account of the history of scientific exploration of Cerro Guaiquinima and provided a comprehensive description of this mountain and a vegetation map of its summit.

Early in 1990, a party of six zoologists from the American Museum of Natural History participated in the first multidisciplinary expedition to Cerro Guaiquinima, under sponsorship of the Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales in Caracas (FUDECI). Although we had only 12 days on the summit, excellent logistics by the FUDECI staff and helicopter support from the Venezuelan military allowed the gathering of significant collections. Here we report on a collection of 105 amphibians, 5 lots of tadpoles, and 64 reptiles made from February 18 to March 1, 1990, in two summit camps.

ACKNOWLEDGMENTS

We are exceedingly thankful for our Venezuelan friends and colleagues, who exemplify the spirit of international cooperation. For this particular expedition, we single out: Dr. Francisco Carrillo-Batalla, President of FUDECI; Dr. Eugenio de Bellard Pietri, Expedition Leader for FUDECI; Sr. Pedro Pérez Ramírez, Assistant Expedition Leader; and Dr. Antonio Machado Allison, Director, Museo de Biología de la Universidad Central de Venezuela. In addition to his companionship in the field, Dr. Machado Allison was of exceptional help in facilitating our stay in Caracas.

Other American Museum personnel who participated in this trip are Dr. Carl J. Ferraris, Jr., Research Associate in Ichthyology, Dr. David A. Grimaldi, Assistant Curator in Entomology, and Drs. Richard O. Prum and Jeffery Woodbury, both Chapman Fellows in Ornithology. We valued their good humor and help in the field. Participation by the American Museum segment of the Expedition was made possible by a grant from Corresponding Member Kathleen de Phelps of Caracas, and for her we reserve especial gratitude and affection.

For lending comparative specimens in their care, we thank Dr. W. Ronald Heyer, National Museum of Natural History (USNM),

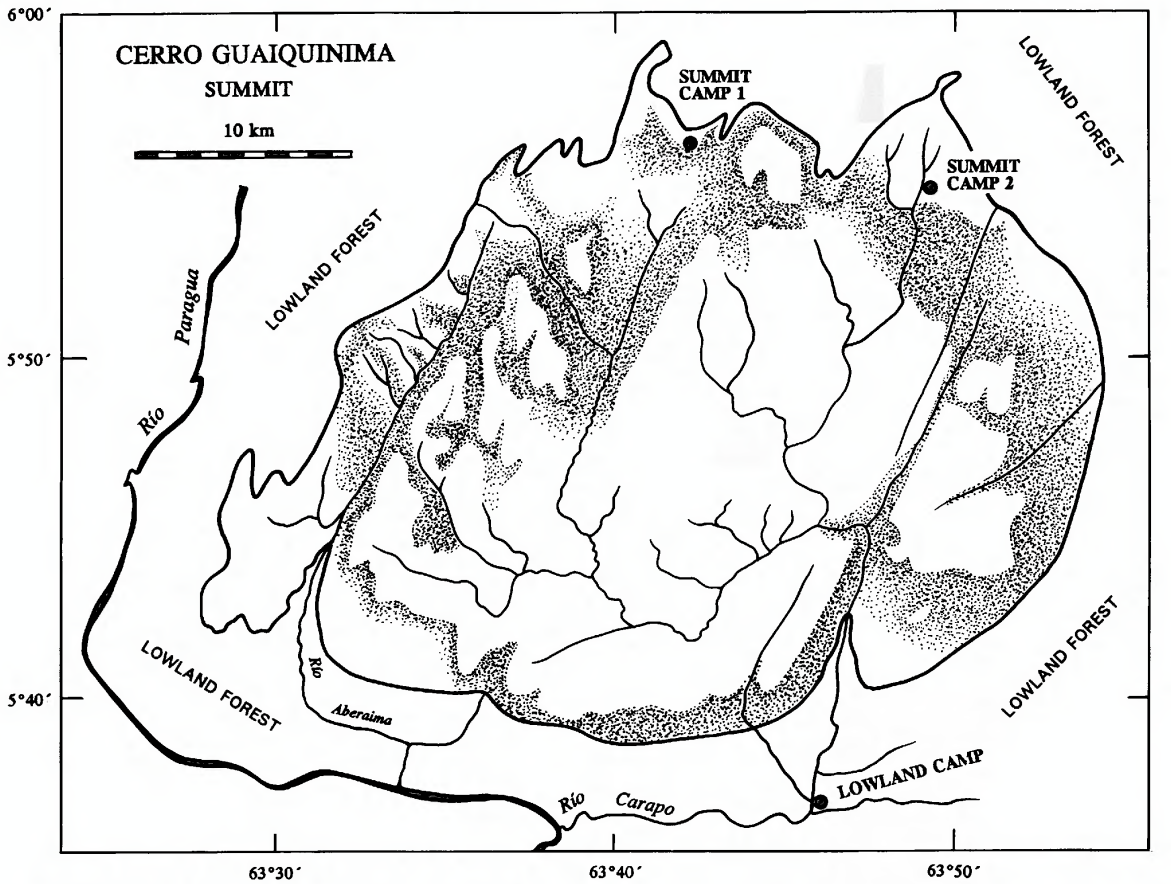

Fig. 1. Summit area of Cerro Guaquinima showing locations of FUDECI Summit Camps 1 and 2 worked by the authors. Patterned area denotes approximate limits of the unusual (for a tepui) high forest; unshaded areas are open-canopy formations, including scrub, "savanna," and sparse woods. Map adapted from Steyermark and Dunsterville (1980: 289).

Dr. Roy W. McDiarmid, National Museum of Natural History (RWM field series), Mr. José Rosado, Museum of Comparative Zoology (MCZ), and Dr. Harold Voris, Field Museum of Natural History (FMNH).

For comments on the manuscript and other help we are grateful to Drs. Darrel R. Frost, Roy W. McDiarmid, and Jay M. Savage.

Deposition of Specimens

In order to prepare this manuscript and for purposes of providing a permanent means of tracking the specimens on which it is based, our collection was cataloged in the separate amphibian and reptile series of the American Museum of Natural History (AMNH) and the specimens are so cited herein. However, a portion of the collection contractually belongs to the Museo de Biología de la Universidad Central de Venezuela (MBUCV), in Caracas. One-half of the collection, including half of the species represented by single specimens, is to be transferred to MBUCV.

THE NATURAL LANDSCAPE

General Features: In spite of its immense area (figs. 1—3), Cerro Guaiquinima, is one of the lowest tepuis in terms of average height of the summit[3] (Steyermark and Dunsterville, 1980). The higher parts of Guaiquinima lie along its western escarpment, with

[3] We follow Steyermark and Dunsterville (op. cit.) in using the word "summit" as essentially synonymous with "mesa," in reference to the upland part of a tepui contained by escarpments. The tepuis are not truly flat-topped but their highest points are often little more than bumps compared with the usual notion of mountain summits.

Fig. 2. The southern escarpment of Cerro Guaiquinima as viewed from helicopter (February 18, 1990).

a peak in the southwestern quadrant reaching the maximum height at 1680 m above sea level. Elevations above 1300 m are briefly attained along the other escarpments. From the western, northern, and eastern escarpments, the rugged landscape is inclined inwardly and southerly, to an elevation of only 700 m at the headwaters of a tributary of the Río Carapo. About 80 percent of the immense summit area drains south through a single outlet to the Río Carapo, a tributary of the Río Paragua. Another 10 percent drains through the Río Aberaima into the Paragua, which flows northward along the western side of Cerro Guaiquinima until it empties into the Río Caroní and finally into the lower Río Orinoco at Ciudad Guayana.

Steyermark and Dunsterville (1980) showed that 40 percent of the summit is covered by an exceptionally tall forest that rings the tepui (figs. 1, 3). The summit of no other tepui is known to support forest this extensive or this tall (25–30 m). The remainder of the summit is characterized by open, xeric vegetational formations, including scrub, sparse woods, and an odd "savanna" vegetation.

ITINERARY AND SUMMIT AREAS COLLECTED: The FUDECI base camp was in Canaima near the Río Caroní. Field parties were ferried by military helicopter from Canaima to a lowland forest camp on the Río Carapo, roughly 120 km to the southwest. The authors arrived separately at the Río Carapo camp on February 16 and 17 and departed to the highland on February 18. The Río Carapo camp was situated at 330 m elevation at the southern base of Cerro Guaiquinima, just downstream from the point where 80 percent of the waters debouch from the summit (fig. 1). Except on low ridges, the forest here is subject to flash-flooding, which must be of frequent occurrence during the wet season. We only over-nighted at the Carapo camp and the few specimens collected do not adequately represent the lowland fauna; only the following species were taken: *Bufo marinus* (no vouchers), *Bufo typhonius* auctorum,

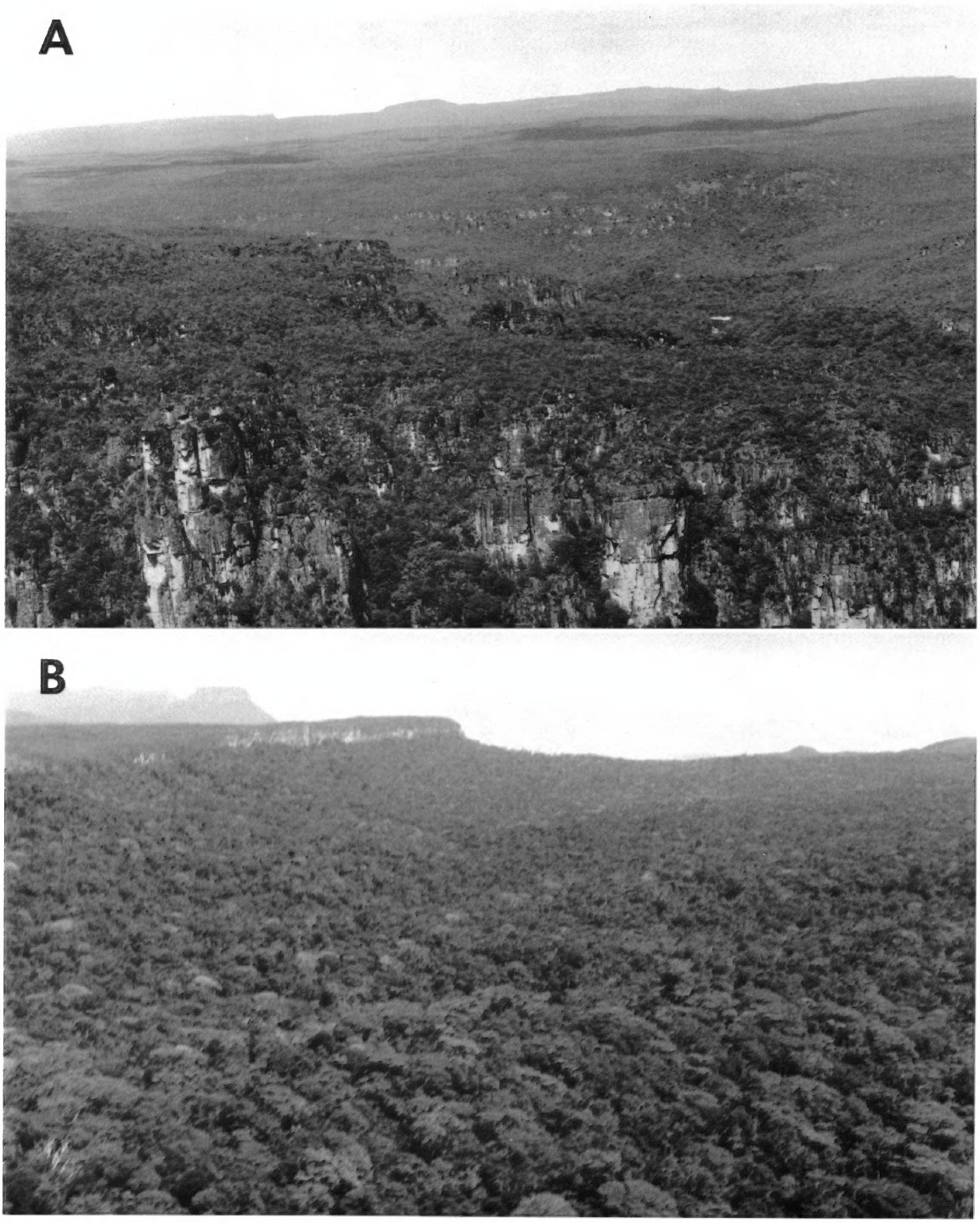

Fig. 3. Views across the top of Cerro Guaiquinima, both from a helicopter flying in a northerly direction (February 18, 1990). **A.** The immense summit area as seen when rising above the south edge of the escarpment. **B.** Northeastern side of the summit, overlooking canopy of tall forest (cf. fig. 1); high ground to the northwest is also part of the summit.

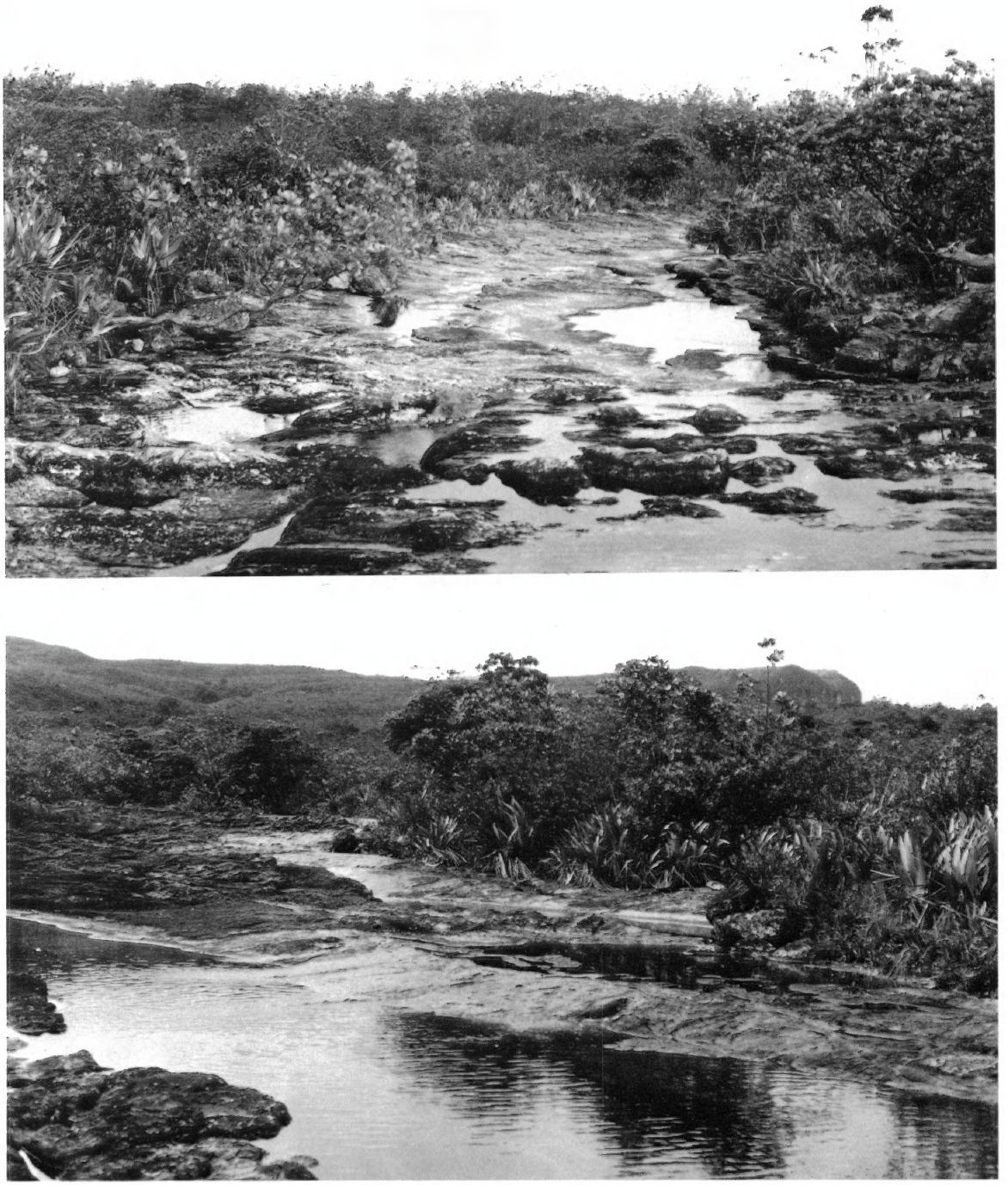

Fig. 4. Views of the unshaded, highy scoured "north stream" in *Stegolepis-Clusia* savanna a few km northwest of Summit Camp 1 (fig. 1; see also fig. 19 for a view farther upstream). Habitat of *Leptodactylus rugosus*, *Neusticurus* sp. (cf. *N. rudis)*, *Liophis torrenicola*, and *Philodryas cordata* (February 28, 1990).

Hyla boans, *Hyla calcarata*, *Leptodactylus wagneri*, *Anilius scytale phelpsorum*, *Geochelone carbonaria*, *Phrynops geoffroanus*.

FUDECI established six summit camps. Owing to limited time, we chose to work only in camps 1 and 2 near the northern escarpment (fig. 1). We arrived first at Camp 2 and stayed there until a drying water supply and

Fig. 5. Views of "south stream," at the edge of tall forest a few km west of Summit Camp 1. The mouth of the "small forest stream" can be seen in the lower view (February 1990).

relatively poor collecting caused us to radio for helicopter evacuation; we were in Camp 2 February 18–22. We found an abundance of water and more habitat diversity at Camp 1, where we worked during the period February 22–March 2. At the end of this time, we moved by helicopter directly to base camp at Canaima.

Description of Summit Camp 1

The FUDECI Summit Camp 1 (1030 m elevation) was situated at the edge of tall forest between two eastward-flowing streams, a short distance above their confluence. The outermost stream (i.e., the one nearest the escarpment) is hereafter referred to as the *north stream*. The innermost stream is hereafter referred to as the *south stream*, and a minor, north-flowing tributary is referred to as the *small forest stream*. The more-or-less parallel-flowing north and south streams are ecologically quite different, as discussed below.

Steyermark and Dunsterville's (1980) vegetation map shows tall forest extending to the edge of the escarpment in places, but at least in the vicinity of Camp 1 there actually is a belt of scrubby *Stegolepis* (Rapateaceae) and *Clusia* (Clusiaceae) savanna along the rim of the tepui. The north stream flows unshaded through this formation (fig. 4). This stream has a highly scoured bed in which solid sandstone alternates with bottom sections composed of a rubble of small to large rocks. There are no deposits of small gravel and no organic or inorganic sediment beds whatever; search revealed only an occasional thin patch of new sand occupying but a few cm^2—obviously newly derived from nearby sandstone. Clearly the north stream flows torrentially and dangerously during periods of intense rainfall, as also evidenced in one place where a rock of some size ($\approx$ 0.5 m diameter) was wedged in the crotch of a tree about 2 m above stream edge. The north stream comes from higher ground to the west, in an area of waterfalls and open-canopy forest with some moderately tall (about 20 m) trees, bromeliads, and palms.

Several kilometers west of camp, south stream emerges from the scrubby vegetation to become very different as it courses through the edge of the tall forest or through the forest-savanna ecotone (fig. 5). This long section of south stream differs markedly from the parallel north stream in two major respects: (1) south stream is shaded under a canopy during this course; and (2) its bed is not scoured as in the north stream. Although clearly torrential at times, the south stream's bed is more often sand and/or organic silt rather than sandstone or rock rubble, and the stream is sometimes blocked by fallen trees. We attribute this difference to the influence of forest on runoff rather than to gradient, inasmuch as small waterfall drops of $\geq$ 1 m seem as frequent in the south stream as in the north one.

The tributary designated as "small forest stream" ($\leq$ 1 m wide) flows from dense, brushy forest into the main channel of the south stream (fig. 5, lower). West of the small stream, the forest habitat gives way to savanna vegetation. East of Camp 1, south and north streams merge and flow though savanna, but this larger stream must eventually reenter the belt of tall forest.

The ecotone between scrubby savanna and forest is narrow ($<$ 10–15 m), being marked by some tall grass among the woody vegetation, scattered *Heliconia* along parts of the south stream, and a few *Cecropia* away from the stream.

The tall forest south of Camp 1 has a canopy estimated at 25–30 m, is nearly evergreen (no more than 5–10 percent deciduous in late February) and is curious because its high canopy occurs in combination with high elevation (1000 m) and a well-developed false or second floor.[4] The tall straight tree trunks are moderately mossy. There are scattered large bromeliads both on trunks and on the ground, but none held water when examined in late February. There are tree ferns and palms, including stilt palms and spiny palms. Moderate machete work is needed to move through some places, especially near small streams, but the forest is relatively open on hillsides where there is little brush or herbaceous vegetation. A "second floor" is well developed at least throughout this area of tall forest. It is composed of a dense mat of roots and organic matter and, although it looks like solid ground, one could always poke a stick (and sometimes a foot) through it. A Venezuelan team headed by Juan Brandín estimated an average thickness of the false floor as 25 cm; the false floor is elevated up to at least 0.5 m above a sand base (the true floor).

[4] In the Neotropics, a second floor is perhaps most likely to occur on exposed ridges or mountain tops in cloud forest of the elfin woodland type, where the canopy is less than 10 m (e.g., Myers, 1969: 18, 32).

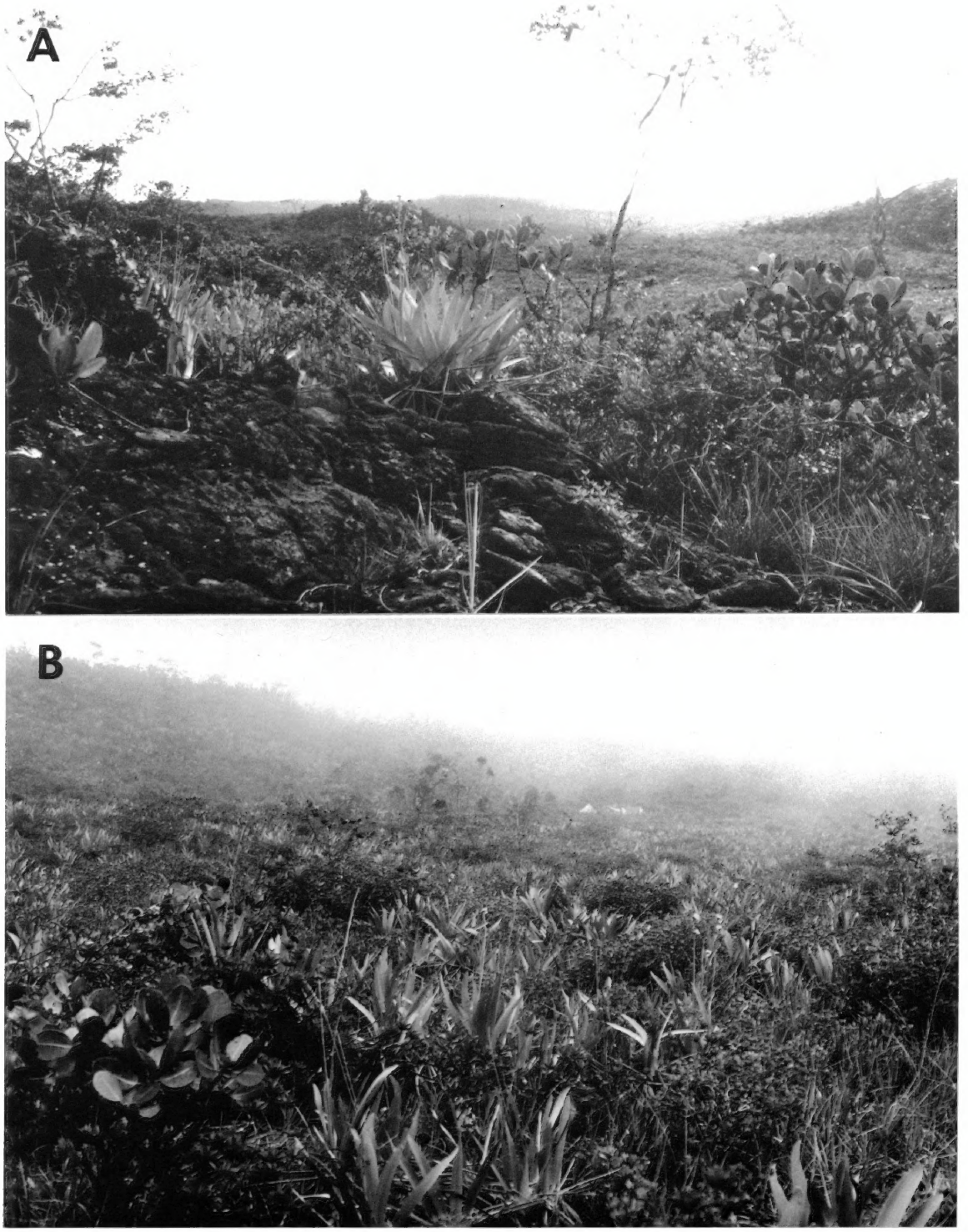

Fig. 6. **A.** View from the rocky northeastern rim looking westerward into a basin of *Stegolepis-Clusia* savanna, on the summit of Cerro Guaiquinima. **B.** Closer view of the savanna at Summit Camp 2 (February 19, 1990). The abundant plant with straplike leaves is *Stegolepis squarrosa*, which is endemic to Cerro Guaiquinima; the broadleaf small tree at the lower left is *Clusia*. Habitat of *Ameiva ameiva* and *Tropidurus hispidus*.

Fig. 7. Drying stream bed in savanna at Summit Camp 2 (February 21, 1990). **A.** Deep pool at head of stream. **B.** Rocky bed a short distance downstream. Habitat of *Hyla minuta*, *Leptodactylus rugosus*, and *Neusticurus* sp. (cf. *N. rudis*).

Description of Summit Camp 2

FUDECI Summit Camp 2 (1150 m elevation) was situated in a depression bordered by the northeastern escarpment (fig. 6A). This region of the summit is in what Steyermark and Dunsterville (1980: 292, fig. 4a, b) described as,

> a very large (about 25 km²) patch of savanna . . . Although referred to here as "savanna," these expanses of low vegetation are not grassy savannas of the usual type, but bear a special flora whose growth forms resemble savanna-like vegetation.

The broad-bladed *Stegolepis squarrosa* (Rapateaceae) is a dominant along with some low woody shrubs, including *Clusia* (fig. 6); there is much exposed sandstone. Other habitats collected were dry sandstone stream beds and nearly isolated pools in a small, drying, southerly flowing stream, which also was the camp water source (fig. 7). On one morning, there was cloud cover, mist, and light rain, but otherwise the entire area was sun-exposed during our stay. Morning air temperature was about 16°C, daytime shade 26°C and higher, and ground surface in the sun about 40°C.

SPECIES ACCOUNTS

Frogs

FAMILY HYLIDAE

Hyla benitezi Rivero

Figures 8–10

Hyla benitezi Rivero, 1961: 116–118, fig. 9. Holotype MCZ 28564 from Caño Wanadi, Mt. Marahuaca, Amazonas, Venezuela, collected by J. A. Rivero, May 20, 1950.

Material: AMNH 133843–133854 (9♂, 3♀), Summit Camp 1.

Natural History: These frogs were collected in forest at night, mostly along the south stream and its tributary the small forest stream; one specimen was found at an additional small stream in the tall forest. They were perched on leaves 1–2 m above water or on rock faces near small waterfalls. Three males were calling from rocks near a waterfall, a site similar to that reported for the species from Cerro Marahuaca (Rivero, 1961) and Cerro Duida (Rivero, "1971" [1972]). Rivero ("1971" [1972]) heard the call as a series of relatively low and liquid sounds.

Calls of *H. benitezi* were recorded between 2020 and 2030 h. on February 24, 1990, at a waterfall in the south stream. Advertisement calls of two ($N = 1$), three (1), and four notes (3) were recorded. A sound spectrograph of the four-note call is shown in figure 10A; notes are 0.02–0.04 sec in duration ($\bar{x} = 0.023$ sec), with an average of 0.113 sec between notes; the last note in the call is shorter than the first three notes.

We also recorded five duets, an example of which is shown in figure 10B. The frog (AMNH 133844) whose call is described above gave a slightly different call when a second male was calling nearby (cf. fig. 10A, B). The average duration of each note becomes longer (0.054 sec), the average interval between notes slightly shorter (0.104 sec), and the notes are modulated, with the dominant frequency changing from 2200 to 2500 Hz. More notes are given during duets than when males call alone.

Color Pattern: In life, the dorsum was brown with dark brown cross-lines, or brown with distinct pale yellow dorsolateral stripes and dark brown dorsal markings. One individual was pale brown at night; by day it was green dorsally with blackish brown canthal and dorsolateral stripes. There were dark brown markings on the limbs. The throat and venter were white with or without a variable amount of orange suffusion. One frog differed from all others in having the throat and chest medium blue green; Rivero ("1971" [1972]) observed this unusual ventral coloration in frogs from Cerro Duida. The undersides of the limbs were gray, suffused with orange or bright orange. The hands, feet, and webs were light to bright orange. The iris was pale tan with sparse, fine, dark venation and vague gray or grayish brown horizontal stripes.

In preservative, the dorsum is tan, light brown, brown, or gray brown. One frog has broad pale dorsolateral stripes from the tip of the snout, over the eye, to the sacrum; all specimens except AMNH 133847 have fine dark brown dorsolateral lines. A thin dark brown canthal stripe is present in all but four examples. A thin interorbital stripe is present, incomplete, or absent. Fine weblike transverse dorsal lines are present in all frogs except two; AMNH 133854 had three transverse dark brown blotches outlined in black and AMNH 133844 has a large dark brown dorsal blotch. The arms are distinctly barred,

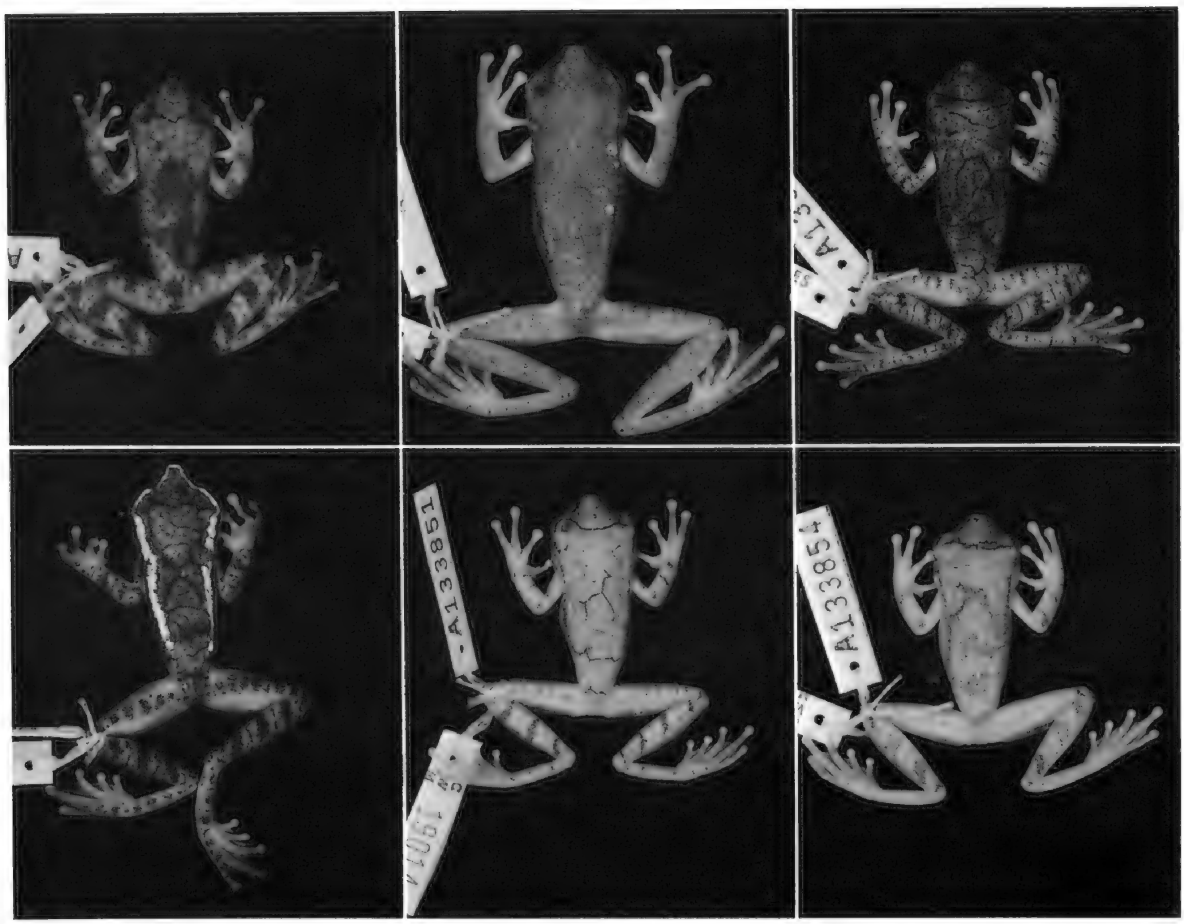

Fig. 8. Color pattern variation in a population sample of *Hyla benitezi* from Cerro Guaiquinima, all ×0.87. Top row, from left to right: AMNH 133844, 133845, 133848. Bottom row: AMNH 133849, 133851, 133854.

indistinctly barred, or lack bars. The anterior thigh is immaculate or lightly peppered; the dorsal thigh is distinctly barred, indistinctly barred, spotted, or heavily peppered; the posterior thigh is immaculate or peppered. The dorsal tibia has alternating thick and thin bars, thick bars, thin bars, or lacks bars. The dorsal surface of the tibiofibula and foot has distinct barlike spots, indistinct spots, or lacks spots. The ventral surfaces are dirty white, dirty yellow, or yellow. The lower lip is white with varying amounts of peppering; peppering heaviest near jaw angle. Finger I and toe I lack pigment in all but two frogs; finger IV and toes IV and V are pigmented in all examples. The toe webbing is pigmented or lacks pigment; in those individuals with pigmentation in the webs, it is heaviest between toes IV and V.

REMARKS: *Hyla benitezi* may be a Venezuelan endemic. It is known from two localities in Amazonas Territory (Cerro Marahuaca and Cerro Duida) and now also from Cerro Guaiquinima in Estado Bolívar. In the original description of *H. benitezi*, Rivero (1961) stated that the snout was subovoid. In the Cerro Guaiquinima sample, the snout is rounded to truncate in dorsal profile and rounded in lateral profile. We examined the holotype (MCZ 28564), and the snout is truncate in dorsal profile (fig. 9). The tongue in the holotype is circular, notched posteriorly, and adherent; in the Guaiquinima sample, the tongue is notched or entire. Rivero (1961) described the vomerine teeth as being / \-shaped and later mentioned a specimen in which these teeth were arched (Rivero, "1967" [1968]). In the Guaiquinima sample,

Fig. 9. Holotype of *Hyla benitezi* Rivero from Cerro Marahuaca, Venezuela (MCZ 28564), ×1.4.

the vomerine teeth are arched, slightly arched (133844), / \-shaped (133843, 133851, 133853), or bilaterally asymmetrical (arched on the left and diagonal on the right in 133847). Rivero (1961) reported that the diameter of the eye was more or less equal to the eye-nostril distance; in the holotype and in the Guaiquinima frogs, the eye diameter exceeds the eye-nostril distance (table 1). Rivero (1961) described the tympanum as small, indistinct, and one-third the eye diameter. In the holotype, the diameter of the tympanum is 24.3 percent of eye diameter and the tympanum is concealed (visible in outline) under the skin. In the Guaiquinima sample, the tympanum also is visibly concealed and is 27–42 percent of eye diameter (table 1); it is separated from the eye by more than 50 percent of its diameter. Rivero (1961) noted the external rudiment of the pollex in

TABLE 1

Size and Proportions of Adult *Hyla benitezi* from Cerro Guaiquinima, Compared with the Holotype from Cerro Marahuaca

(Values are means − 1 SD, with ranges in parentheses)

Character	Males (N = 9)	Females (N = 3)	Holotype Adult ♂
Snout-vent length (SVL) in mm	33.83 ± 1.600 (31.0—36.0)	42.00 ± 5.568 (36.0—47.0)	36.0
Head length/SVL	0.392 ± 0.008 (0.38—0.40)	0.357 ± 0.043 (0.32—0.40)	0.388
Head width/SVL	0.389 ± 0.007 (0.38—0.40)	0.357 ± 0.043 (0.32—0.43)	0.388
Tibia length/SVL	0.529 ± 0.014 (0.51—0.55)	0.529 ± 0.058 (0.47—0.58)	0.542
Foot length/SVL	0.411 ± 0.011 (0.39—0.43)	0.415 ± 0.031 (0.38—0.44)	0.403
Tympanum/eye	0.367 ± 0.059 (0.27—0.42)	0.375 ± 0.030 (0.34—0.40)	0.243
Eye—naris/eye	0.853 ± 0.054 (0.76—0.91)	0.865 ± 0.147 (0.75—0.95)	0.878

the holotype. We examined x-ray photographs of Guaiquinima specimens and found this character to be sexually dimorphic—males have a distinct pollical swelling with a large concealed spine, whereas the females have a smaller pollical swelling with a small concealed spine. In the original description, Rivero wrote that the finger discs were larger than the tympanum and toe discs. In the Guaiquinima sample, the finger discs are larger than the toe discs, but are smaller than the tympanum. Rivero (1961) described the subarticular tubercles as small and rounded; he later (Rivero, "1971" [1972]) noted that the distal subarticular tubercles on the hand were divided. In frogs from Guaiquinima, the distal tubercles of fingers I and II are prominent, rounded and entire except in AMNH 133845 where the tubercle of finger I is distally bifid on the left hand. The tubercles are bifid under fingers III and IV except in AMNH 133844, where the tubercles are bifid on the left and distally divided on the right. In AMNH 133848, the first finger on the left hand is abnormally short; the subarticular tubercle is wider than the disc, and the width of the disc (0.9 mm) is less than the width of

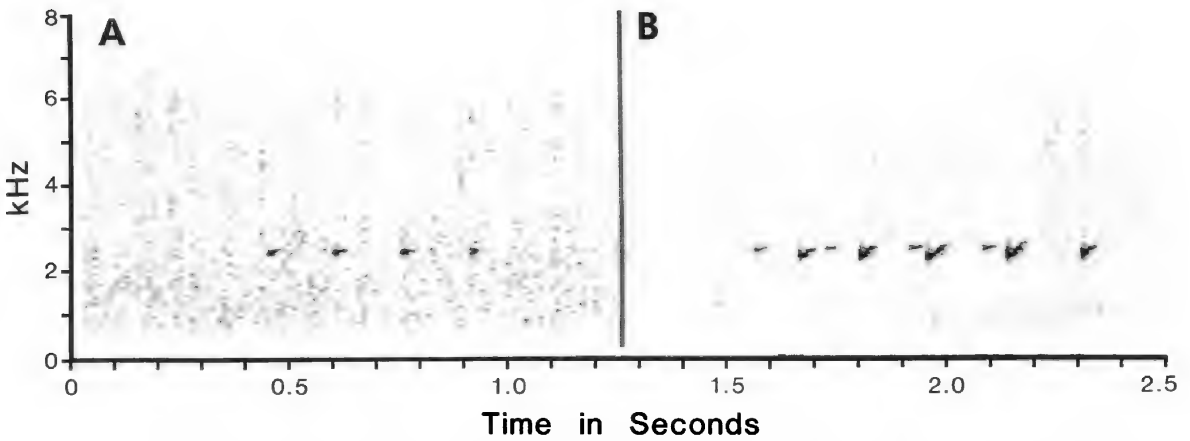

Fig. 10. Vocalizations of *Hyla benitezi* graphed with 45 Hz narrow-band filter (from AMNH herpetology reel 257): **A.** A four-note advertisement call of AMNH 133844. **B.** A duet, including same frog as in A (foreground notes showing rising frequency) responding to another individual calling normally in background. Recorded February 24, 1990; air temperature 18.6° C.

the disc on the right hand (1.4 mm). The pollical swelling on the left hand of 133848 is the same size as that of the right hand. Rivero (1961) noted that the inner metatarsal tubercle is elongate, flat, and indistinct; in the Guaiquinima sample, the tubercle is elliptical, flat, and distinct.

Females of *H. benitezi* from Guaiquinima are larger than males (table 1). In all frogs, the anal sheath is short; the vent opens at the upper level of the thighs; and there are white tubercles on the thighs ventral to the anal sheath. The anal ornamentation consists of two white vertical ridges with dense tubercles lateral to them. Small tubercles are also present on the heels. All frogs have a ridge of low, white tubercles on the ventrolateral surface of the arm that extends from the elbow to the disc on finger IV. All examples have an outer ridge of low white tubercles from the heel to the disc of toe V, and five specimens also have an inner ridge of tarsal tubercles. In males, the vocal slits extend from opposite the middle of the tongue to the angle of the jaw. All specimens have a low supratympanic fold from the tympanum to the insertion of the forearm.

Hyla minuta Peters

Figures 11, 12

Hyla minuta Peters, 1872: 680. Six syntypes from Neu-Freiburg [Nova Friburgo, Estado Rio de Janeiro] and two from vicinity of Rio de Janeiro [city], Brazil.

MATERIAL: AMNH 133855–133867, 133868–133872 (tadpoles), Summit Camp 2.

NATURAL HISTORY: All frogs (12♂, $\bar{x}$ = 24.96 mm SVL; 1 juvenile, 16 mm SVL) were taken at night at headwater pools (fig. 7) of an otherwise rapidly drying stream. Measurements and proportions for this sample are summarized in table 2. Five lots of tadpoles were collected by day in the same pools (water temperature at 1430 h. was 31°C). *Hyla minuta* was the only anuran heard calling at the site; calling began at dusk and continued until approximately 2200 h. Males called from vegetation (primarily *Stegolepis*) surrounding the pools. Calling from the edges of small ponds has been reported for *H. minuta* in Venezuela (Heatwole et al., 1965; Rivero, 1961, 1969; Rivero and Esteves, 1969), Trinidad (Kenny, 1969), and Brazil (Bokermann, 1963; Duellman, 1978). One male (133859) was recorded between 2035 and 2055 h. on February 19—a cool windy night (air 16.6°C) when calling activity was much reduced; it was the only one calling in the area. Twelve advertisement calls, each consisting of a single note, were recorded (fig. 11A). Each note has an average duration of 0.1 sec; dominant frequency is between 3500 and 4000 Hz; notes are given at a rate of about 144 pulses/sec, with an average interval of 18.3 sec between notes.

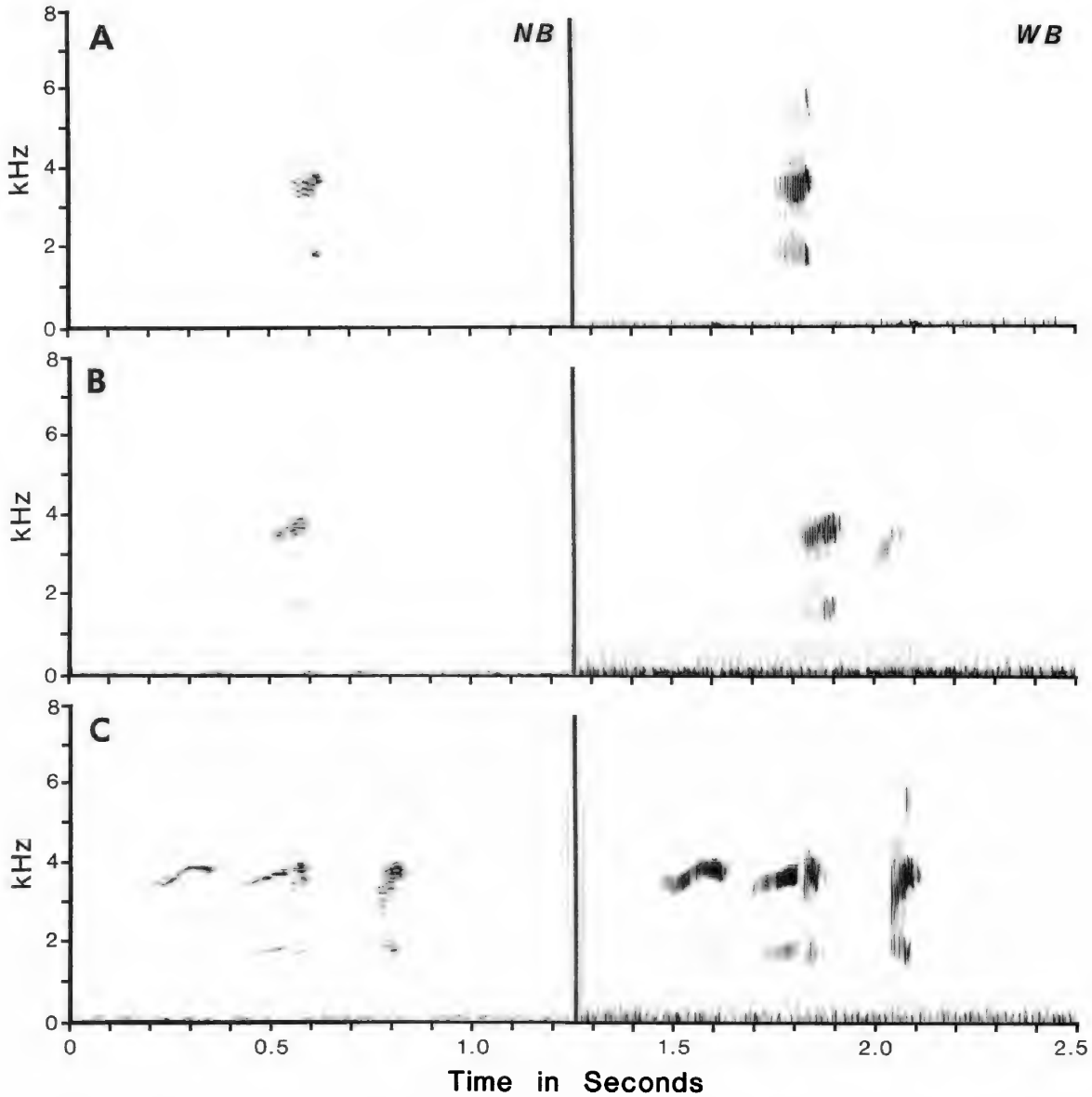

Fig. 11. Vocalizations of *Hyla minuta* graphed with both 45 Hz narrow-band and 300 Hz wide-band filters (from AMNH herpetology reel 257): **A.** Advertisement call of AMNH 133859 (Feb. 19, 1990, air 16.6°C). **B.** Two-note call of AMNH 133862 (Feb. 20, 1990, air 20.4°C). **C.** Complex call of either AMNH 133861 or 133862 (Feb. 20, 1990, air 20.4°C).

Two additional males (AMNH 133861, 133861) were recorded between 2025 and 2100 h. on the following much warmer night (air 20.4°C) when several frogs were calling. Both males recorded gave advertisement calls similar to those of AMNH 133859 above, except that, at the warmer temperature, the calls were slightly longer, slightly faster (averages of 154 and 167 pulses/sec), and were repeated more frequently (average internote intervals of 11.1 and 14.7 sec.

In addition to the advertisement call, AMNH 133862 gave a two-note call (fig. 11B): Both notes rise slightly in frequency, but with the first one resembling the advertisement call in duration and dominant frequency and with the second note being about half as long and lower pitched. We assume that these two-

note calls are encounter or aggressive calls; one was emitted 0.67 sec after an advertisement call by AMNH 133861.

A more complex call of 3–4 notes also was recorded (fig. 11C): The first one or two notes are very rapidly pulsed and rise in frequency between 3500 and 4000 Hz, with or without a slight fall at the end. The first one or two notes are narrowly tuned, in contrast to the last two notes, which are structured more like (albeit shorter than) the two-note encounter call (cf. fig. 11B, C). Cardoso and Haddad (1984) studied calling behavior in three Brazilian populations of *Hyla minuta;* their plate (fig. 2) of aggressive calls shows notes structurally similar to the two kinds of notes in the complex Venezuelan call in our figure 11C (but see below).

Rivero (1969: fig. 2) published a sound spectrograph for *Hyla minuta* from the La Escalera region in Estado Bolívar, Venezuela (recorded in May, without temperature data). His illustration differs from ours in that the notes are a bit longer and given at a higher frequency (about 4000–4500 Hz).

Wide-band sound spectrograms available for *Hyla minuta* from southern Brazil show higher dominant frequencies than those from Venezuela.[5] Dominant frequency appears highest in calls recorded at the type locality (Nova Friburgo near Rio de Janeiro)–roughly between 5000 and 6000 Hz (Cardoso, MS: fig. 16B; Cardoso and Haddad, 1984: fig. 1, upper).

Duellman (1978: 156) described the call from northern Brazil (Belém) as a "harsh primary note, followed by 1–3 shorter secondary notes, repeated at a rate of 8–13 . . . per minute," with a dominant frequency of 3200 Hz. Duellman's recordings possibly were of complex aggressive calls. In any case, there clearly are considerable differences in sound spectrograms and call descriptions ascribed to *Hyla minuta* (see Remarks).

[5] An exception is Bokermann's (1967: fig. 3) narrow-band sound spectrograph for *Hyla minuta* from Campos do Jordao, Estado São Paulo. With a dominant frequency little over 2000 Hz, this seems unlikely to be the same species as the one recorded at the type locality of *minuta* (see above). As used here "dominant frequency" is simply that part of the note showing greatest energy concentration. Frequency resolution can only roughly be estimated from spectrograms produced with wide-band filters, which are best used for time resolution and relative differences in pulsation.

TABLE 2
Size and Proportions of *Hyla minuta* from Cerro Guaiquinima
(Values are ranges followed by means in parentheses)

Character	Males (N = 12)	Juvenile (N = 1)
Snout-vent length (SVL) in mm	23.5—26.0 (24.96)	16.0
Head length/SVL	0.35—0.39 (0.366)	0.38
Head width/SVL	0.35—0.40 (0.379)	0.38
Tibia length/SVL	0.51—0.56 (0.536)	0.56
Foot length/SVL	0.39—0.50 (0.422)	0.43
Tympanum/eye	0.40—0.58 (0.459)	0.38

COLOR PATTERN: In life, adults were pale to light brown with vague darker brown markings dorsally (see below); thighs dull orange, anal and calcar lines white. Fingers dull orange and toes brown with orange tips; toe webbing light brown with faint orange suffusion. Vocal sac greenish yellow with variable amount of orange suffusion; venter white with variable amount of orange suffusion. The bones were orange. The juvenile specimen was gray with a white venter, light gray thighs, and orange digit tips. The color in life generally agrees with that described by other workers (Cochran, 1955; Rivero, 1961; Bokermann, 1963; Heatwole et al., 1965; Kenny, 1969; Cochran and Goin, 1970; Duellman, 1978).

In preservative, the dorsum is uniform light brown or has such dark markings as an interorbital bar or spot, posterior chevrons, hourglass figure, sacral spots, and/or indistinct blotches. The calcar and anal stripes are distinct or indistinct; one has calcar but no anal stripes and another lacks both. The venter is pale yellow with brown suffusion on the thighs. The juvenile has a uniform grayish brown dorsum; the thighs are tan with brown dots and the lower arms and legs are gray-brown with light (unpigmented) spots; the calcar lines are present, the anal stripe absent;

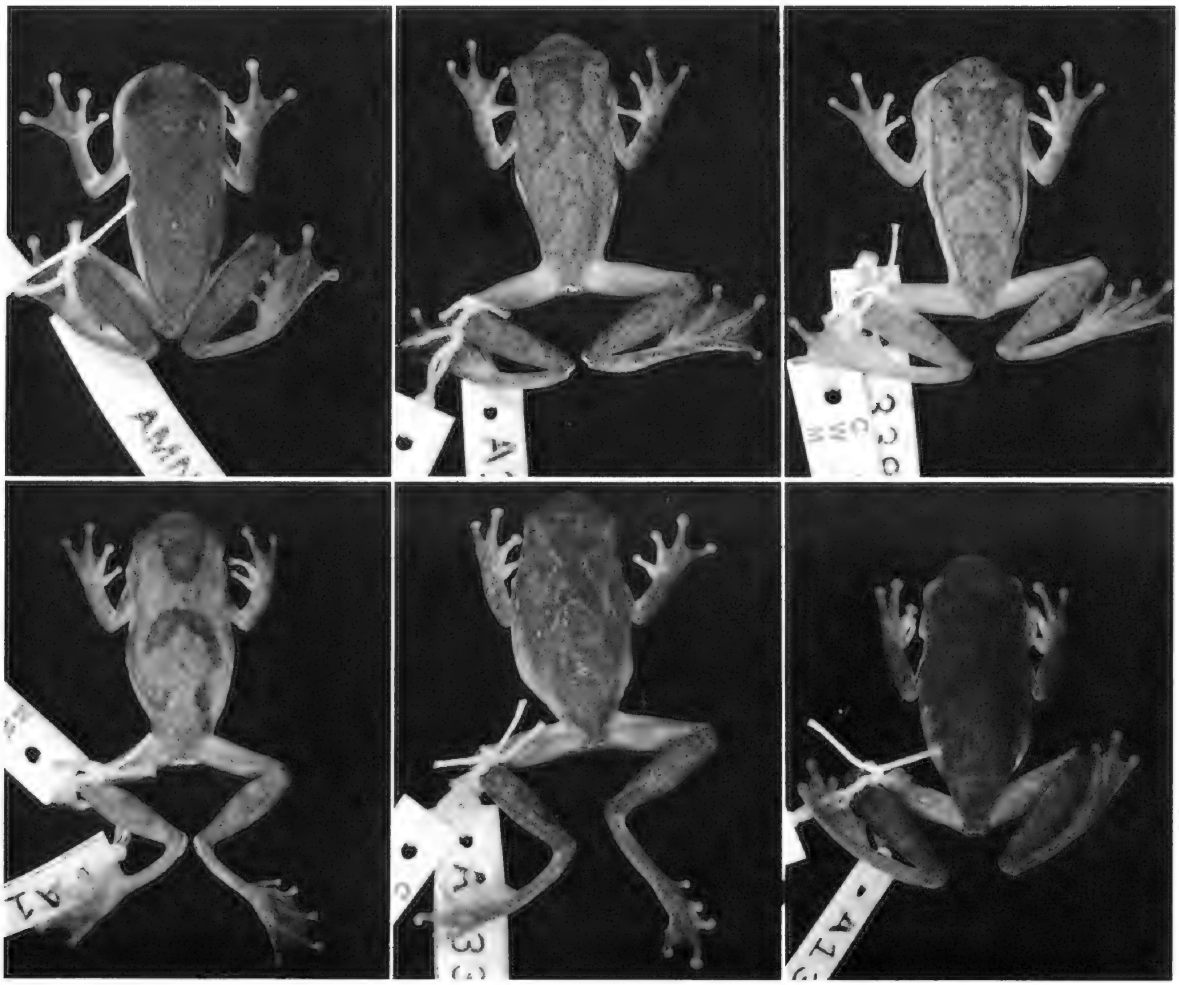

Fig. 12. Color pattern variation in a population sample of *Hyla minuta* from Cerro Guaiquinima, all ×1.4. Top row, from left to right: AMNH 133858, 133861, 133862. Bottom row: AMNH 133863, 133864, 133867.

the tail remnant is a dark gray flap (1.6 mm long, 2.7 mm wide). The palms and soles of all frogs are dark brown.

TADPOLES: The five lots of tadpoles include early and late stages (Gosner, 1960); the number in each stage and measurements are summarized in table 3. The tadpoles resemble those described by Kenny (1969), Heatwole et al. (1965), and Vizotto (1967), and differ from those described by Bokermann (1963) and Duellman (1978) in having one anterior and two posterior rows of labial teeth.

The mouthparts of *Hyla minuta* tadpoles from Guaiquinima resemble those of *H. carnifex* (Duellman, 1969) and *H. columbiana* (Duellman and Trueb, 1983). These three species are the only Neotropical hylids known to have a tooth row formula of 1/2 (Duellman and Trueb, 1983; Altig and Johnston, 1986). In early stages (late 24 and early 25), the P1 row is fully keratinized, the A1 row has a few or no teeth, and the P2 row is frequently not keratinized. The submarginal papillae are not developed completely until stage 26. In early stages, the jaw sheaths are serrated, the upper arch-shaped sheath is fully keratinized, and the lower sheath is incompletely keratinized basally. The sequence of tooth row keratinization is P1–A1–P2. In later stages, the P2 row has fewer teeth than the A2 and P1 rows; the P1 row has the greatest number of teeth. A similar sequence of keratinization has been

TABLE 3
Measurements (in mm) of *Hyla minuta* Tadpoles from Cerro Guaiquinima
(Values are means followed by 1 SD in parentheses when $N > 1$)

Stage	N	Body length	Body width	Body depth	Tail length	Total length	Tail/ total length	Oral disc width
24 late	1	3.2	2.6	2.5	—	—	—	—
25 early	30	5.35 (0.635)	3.65 (0.388)	3.69 (0.482)	10.41[a] (1.087)	15.85[a] (1.636)	0.657[a] (0.019)	1.10 (0.129)
25	38	7.82 (1.092)	4.94 (0.650)	5.22 (0.830)	14.46[b] (2.738)	22.37[b] (3.772)	0.644[b] (0.020)	1.52 (0.185)
25 late	9	9.83 (1.034)	6.13 (0.686)	6.75 (0.754)	20.08[c] (2.537)	30.30[c] (3.159)	0.662[c] (0.019)	1.83 (0.122)
26	9	10.99 (0.704)	6.84 (0.515)	7.57 (0.436)	20.56[d] (2.555)	31.54[d] (3.195)	0.651[d] (0.018)	1.96 (0.133)
27	2	13.30 (0.000)	8.15 (0.212)	8.30 (0.424)	26.75 (1.768)	40.04 (1.768)	0.668 (0.015)	2.30 (0.141)
28	3	13.57 (0.814)	8.33 (0.351)	9.10 (0.361)	30.25[e] (3.182)	44.10[e] (4.101)	0.686[e] (0.008)	2.20 (0.100)
30	1	13.70	8.80	9.50	29.00	42.70	0.679	2.30
33	1	12.80	8.30	8.80	—	—	—	2.40
35	1	13.70	9.10	9.60	25.00	38.70	0.642	2.40
36	1	15.20	9.70	11.30	31.00	46.20	0.671	2.60
40	1	14.30	8.00	7.60	30.00	44.30	0.677	2.30
42	1	12.00	5.80	5.50	25.00	47.00	0.532	2.20

N = [a] 22, [b] 29, [c] 5, [d] 8, [e] 2.

reported in a dendrobatid (Donnelly et al., 1990) and differs from that of *Hyla chrysoscelis* (Thibaudeau and Altig, 1988). The stage 40 specimen has complete mouthparts; by stage 42, the mouth opening is a 2.2 mm wide slit and there are remnants of the papillae at the sides of the opening.

Larval color also changes ontogenetically. In early stages, the dorsum is tan with brown mottling or spots; the lateral body transparent with brown pigment on the organs; the venter transparent with scattered brown flecks anteriorly; there is a conspicuous black mark at the ventroposterior margin of the body

near the fin. A conspicuous stripe runs from eye to eye across the snout. By stage 26, the lateral and ventral skin is opaque; the dorsum brown; the dorsolateral surface brown; the ventrolateral surface white with brown spots or stripes; the ventral body white with brown spots anteriorly. The tail in stages 24–26 is tan with black flecks and fine venation. The fins are conspicuously spotted by stage 36; in stage 33, there are a few spots on the edges of the fins. By stage 30, there are semicircular opaque areas above and below the tail musculature posterior to the body. The distinctive black spot on the body and the eye stripe are not conspicuous in later stages. In life, the tail in early stages was orange near the body; in later stages the semicircular areas of the tail were brown, and the iris was golden.

REMARKS: *Hyla minuta* is widespread east of the Andes (Duellman, 1982) but variation in the calls suggest that more than one species may be masquerading under this name. Especially suggestive, for example, is the more than 1 kHz difference in dominant frequency between calls from the Brazilian type locality and from Venezuela (see above). Frogs from Trinidad and Brazil are smaller than those from Venezuela (Rivero, 1961; Kenny, 1969; Lutz, 1973; this sample).

Relationships also remain uncertain. Cochran (1955) placed *H. minuta* in a *minuta* group with seven species (*bipunctata, decipens, elongata* [= *rubicundula* fide Duellman, 1977], *goughi* [= *minuta* fide Duellman, 1977], *leucophyllata*, *nana*, and *werneri* [= *H. microcephala werneri* fide Duellman, 1974]). Cochran defined the group by smooth skin and small body size.

Duellman and Fouquette (1968) suggested that *H. misera* might be allied with other small South American hylids that lack dark pigmentation on the thighs (including *minuta, elongata*, *nana*, and *werneri*), and that all these might be related to the *microcephala* group.

Cochran and Goin (1970) wrote that *H. minuta* was the only member of the group known from Colombia but they did not list group content. Lutz (1973) indicated that *H. minuta* was allied with *H. bipunctata*, a species currently listed in a *rubicundula* group (Frost, 1985). Cei (1980) stated that *H. minuta* and *H. nana* belonged to the *minuta* group.

The tadpole of Venezuelan *H. minuta* resembles those of species in the *columbiana* group more than it does that of *H. nana* (see above). The tadpole of *H. nana* resembles those of taxa in the *microcephala* group (Lavilla, 1990). *Hyla minuta* sensu lato may be the closest lowland relative of the *columbiana* group.

Osteocephalus taurinus Steindachner
Figure 13

Osteocephalus taurinus Steindachner, 1862: 77–80. Type specimen collected by Johann Natterer at Barra do Rio Negro, Brazil.

MATERIAL: AMNH 133842 (Summit Camp 1). An adult female was taken at night at the edge of the tall forest at south stream. It was perched approximately 40 cm aboveground on a tree trunk adjacent to the stream. Measurements (mm): 78 SVL, 28.0 head length, 26.0 head width, 47.0 tibia length, 34.5 foot length, 7.1 eye length, 5.6 tympanum diameter.

COLOR PATTERN: In life, dorsally brown with dark brown markings; ventral surfaces dirty white with small spots and flecks of dark brown on throat and chest; iris yellow with dense pattern of radiating black lines above and below pupil. The bones of the lower leg are bluish green in the preserved specimen.

REMARKS: This is a widespread species throughout lowland Amazonia and the Guayanan region and it usually is readily identifiable by a pale bright yellow or greenish yellow iris, with a conspicuous pattern of nearly vertical (slightly radiating) black lines above and below the pupil. Although the iris pattern of black markings is nearly diagnostic, there does seem to be some interpopulational variation in iris color. Our field notes indicated that the one Guaiquinima specimen had the usual yellow iris, as did USNM (R. W. McDiarmid, personal commun.) and AMNH specimens from the base of Cerro de la Neblina. One (AMNH 124793) from Rondônia, Brazil, had the top of the iris bright green but the lower part was silvery gray. There is no assurance that some of the ob-

Fig. 13. *Osteocephalus taurinus* (AMNH 133852), a lowland species from the summit of Cerro Guaiquinima, ×0.8.

served variation in iris color may not be interspecific in nature.[6]

FAMILY LEPTODACTYLIDAE

Leptodactylus longirostris Boulenger
Figure 14

Leptodactylus longirostris Boulenger, 1882: 240, pl. 16, fig. 3. Lectotype BMNH 76.5.26.4, designated by Heyer (1978: 33), from Santarem, Brazil, collected by Mr. Wickham .

MATERIAL: AMNH 133835, 133836, Summit Camp 1; AMNH 133838, 133839, Summit Camp 2.

NATURAL HISTORY: An adult male was found in the deepest pond at Camp 2 (fig. 7); the other three specimens are juveniles that were found in open situations along rocky streams (figs. 4, 7). Measurements and proportions are in table 4. This species was not calling during our stay.

COLOR PATTERN: In life, the adult male (AMNH 133838) had a median gray stripe bordered by dark brown paravertebral stripes and pale bronze dorsolateral lines; the face

[6] As treated by Trueb and Duellman (1971), *Osteocephalus taurinus* is probably a composite species—at least in central Amazonia—that minimally includes one or more large species and one or more small ones. Microsympatry is demonstrated in the series AMNH 103015–103018, 103021–103029 (eastern Peru), where a small bronze-eyed species was distinguished from larger bronze-eyed and green-eyed "*taurinus*" in the field by iris color, although the iris pattern of black lines is similar.

TABLE 4
Size and Proportions of *Leptodactylus longirostris* from Cerro Guaiquinima
(Values are ranges, mean in parentheses when $N > 1$)

Character	Males ($N = 1$)	Juveniles ($N = 3$)
Snout-vent length (SVL) in mm	39.0	19.5—24.5 (21.00)
Head length/SVL	0.44	0.45—0.49 (0.461)
Head width/SVL	0.36	0.36—0.37 (0.365)
Tibia length/SVL	0.54	0.45—0.53 (0.476)
Tympanum/eye	0.64	0.47—0.61 (0.593)

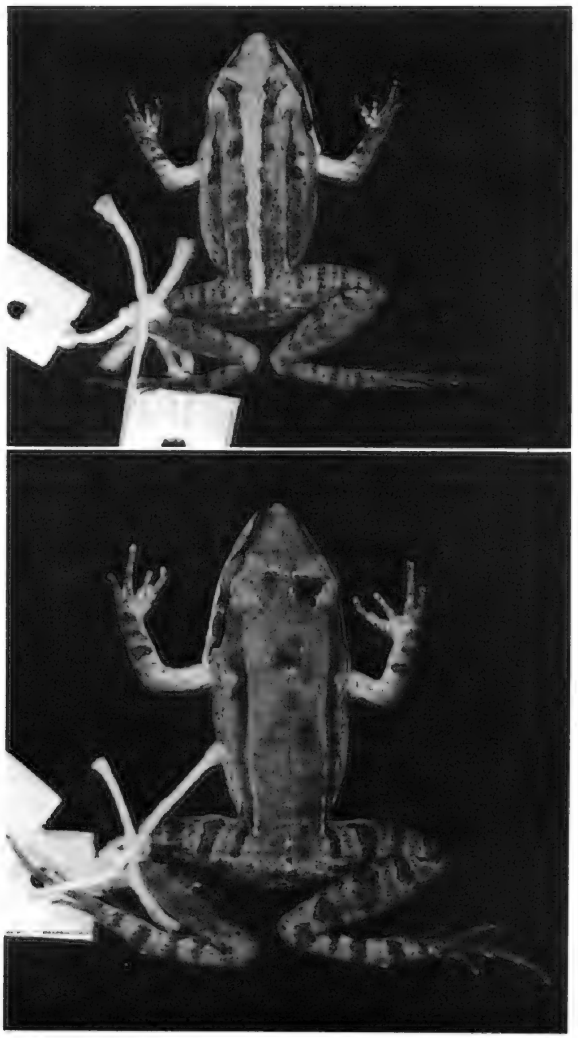

Fig. 14. Color pattern variation in *Leptodactylus longirostris* from Cerro Guaiquinima. Top, AMNH 133836; bottom, AMNH 133835. Both juveniles, ×2.

mask and limb bands were dark brown and there was a horizontal yellow line on the posterior thigh surface. The throat and chest were white, turning yellow on the belly; ventral surfaces of the limbs were pale greenish gray. The upper one-third of the iris was gray with brown venation; the lower two-thirds were suffused with dark brown. One of the juveniles also had a pale middorsal stripe (fig. 14).

REMARKS: Heyer (1978: 61–63) stated that six dorsolateral folds occur when there is a light middorsal stripe in *Leptodactylus longirostris*, but the two striped specimens from

TABLE 5

Size and Proportions of *Leptodactylus rugosus* from Cerro Guaiquinima

(Values are means ± 1 SD with range in parentheses when $N > 1$)

Character	Males ($N = 11$)	Females ($N = 1$)	Juveniles ($N = 37$)
Snout-vent length (SVL) in mm	52.18 ± 4.31 (41.0—55.0)	56.00	25.95 ± 5.08 (19.0—40.5)
Head length/SVL	0.431 ± 0.014 (0.42—0.45)	0.45	0.441 ± 0.025 (0.39—0.51)
Head width/SVL	0.428 ± 0.021 (0.39—0.46)	0.39	0.447 ± 0.019 (0.42—0.50)
Tibia length/SVL	0.488 ± 0.017 (0.46—0.51)	0.050	0.470 ± 0.023 (0.42—0.51)
Foot length/SVL	0.404 ± 0.014 (0.35—0.43)	0.042	0.384 ± 0.191 (0.35—0.42)

Guaiquinima each have four dorsolateral folds. We are following Heyer (op. cit.) and probably Rivero (1971: 6) in using the name *L. longirostris* for a Guayanan species having a distinct transverse pale line or stripe along the posterior face of the thigh (stripe sometimes indistinct in ♂ [20%] but not ♀, fide Heyer, p. 63)—but we express doubt that the specimen designated by Heyer as lectotype of *longirostris* belongs to this species. The lectotype is a female according to Heyer (op. cit.: 32, 61), and it has a different thigh pattern as illustrated in Boulenger (1882: pl. 16, fig. 3),[7] who wrote (p. 240), "hinder side of thighs with a dark brown network."

Leptodactylus rugosus Noble

Figure 15

Leptodactylus rugosus Noble, 1923: 297–299. Holotype AMNH 1169 from near Kaieteur Falls, Guyana, collected August 13, 1911 by F. E. Lutz.

MATERIAL: AMNH 133818–133834, Summit Camp 1; AMNH 133786—133817, Summit Camp 2.

NATURAL HISTORY: *Leptodactylus rugosus* was the most abundant amphibian at both

[7] The hind limbs of the specimen in Boulenger's illustration seem sufficiently well spread that a stripe, if present, should be visible. The marking is concealed in the specimens shown in figure 14.

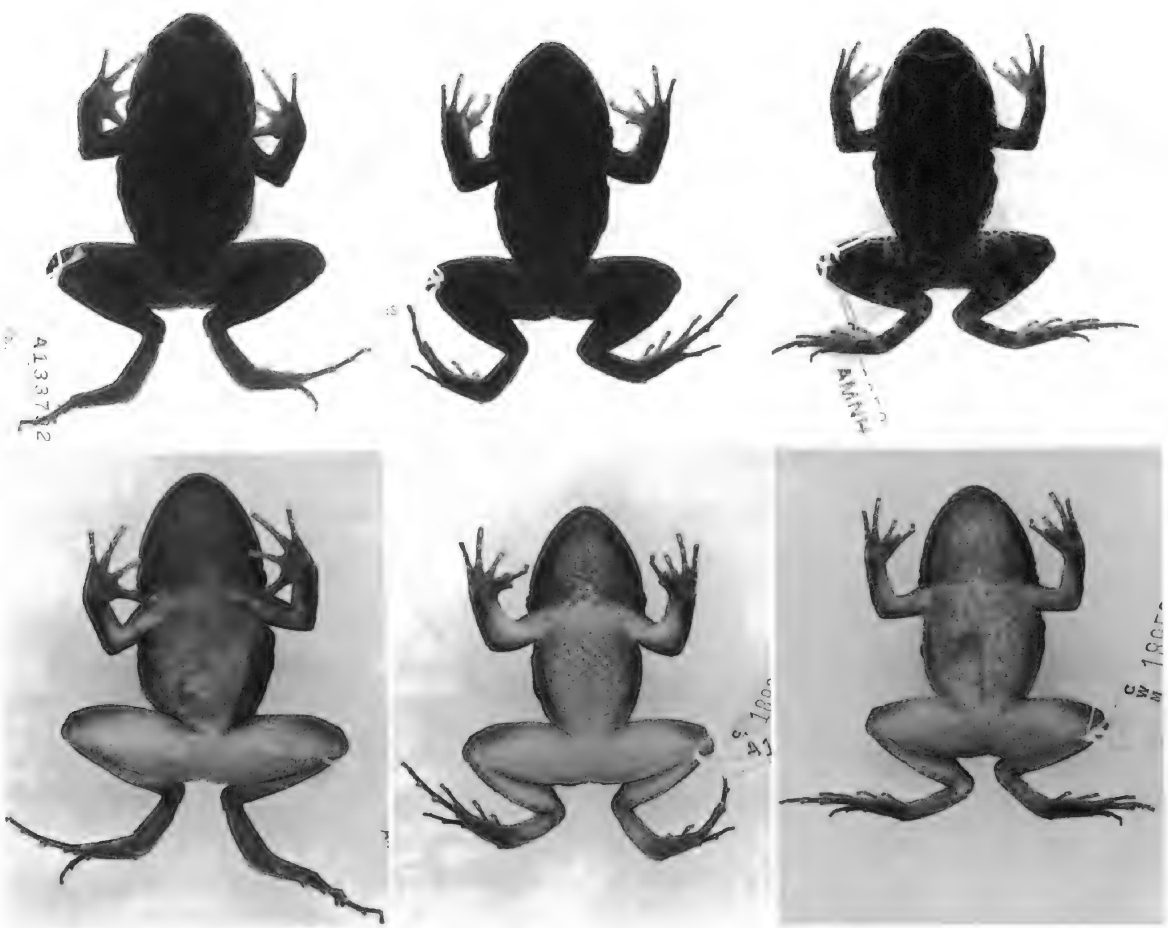

Fig. 15. *Leptodactylus rugosus* from Cerro Guaiquinima. Left to right: AMNH 133792, adult ♀; 133815, adult ♂; 133826, juvenile. Adult ♀ and ♂ ×0.66, juvenile ×0.83.

camps. Adults were taken at night in the rocky stream bed at Camp 2 and in the north stream at Camp 1. At Camp 2, several adults were collected by night in water in the middle of small waterfalls. Juveniles were active both day and night. During the day, juveniles were commonly seen in exposed situations, sitting on rocks around small pools and jumping into the pools when disturbed. There are three times as many juveniles as adults in our sample (table 5) but the proportion of juveniles would be much larger had we not deliberately quit collecting them.

Rivero (1961: 51) has heard *L. rugosus* calling at dusk elsewhere in Venezuela, but there was no evidence of breeding activity during our stay on Guaiquinima. The species occurs perhaps most commonly on outcrops or *lajas* of granitic basement rock and Rivero (loc. cit.) suggested that it is restricted to black crystallized rock of the Guayana highlands. As shown by the Guaiquinima situation, *L. rugosus* occurs also on the Roraima sandstones.

COLOR PATTERN: In life, some juveniles had white-edged dorsal blotches whereas others were uniformly blackish. The throat was heavily marked with gray mottling on white and there was less gray on the venter. The body glands of the groin and the ventral and posterior thigh surfaces had variable suffusion of orange that was bright in some individuals. The iris was bronze above, white on the medial ventral section, and brown between, with dense black venation overall.

In preservative, all frogs have a distinctive

interorbital bar. The dorsum is otherwise uniformly pigmented in 28 specimens (6♂, 1♀, 21 juv.) and spotted or blotched in 21 specimens (5♂, 16 juv.). The dorsal markings of a few individuals are hourglass shaped. The anterior surface of the thigh has few to several irregularly shaped dark brown or black spots. The posterior thigh surface is white or pale orange with distinct black spots or stripes; all individuals have a bright orange gland on the posterior surface of the thigh. The upper tibia is distinctly or indistinctly marked with 2–5 bars in 42 specimens, but the tibia is spotted in seven others. The arms are barred.

In adults and some juveniles, the body gland (situated high on the flanks) extends from the groin anteriorly to the arm, but in some juveniles it extends only to midbody. In the preserved specimens, this gland is either metallic orange (11 adults, 17 juveniles), metallic yellow (1 adult, 19 juveniles), or white (1 juvenile), with irregularly shaped black marks in all.

The upper lip is distinctly or indistinctly marked with 3–4 light lines radiating ventrally from the eye to the lip; one individual had three lines on the right side but the left side of the face was uniformly light. The lower lip is brown with white flecks in all juveniles and the single female, but in males it is dark gray except anteriorly.

The throat is white with brown spots or brown-and-white mottled in juveniles, becoming mostly brown in adults. The belly is dirty white with either a suffusion or spots of brown, being most heavily pigmented anteriorly. The ventral surfaces of the thighs are white, yellow, or orange, with a suffusion or spots of brown in adults. Heyer (1979: 34) stated that the throat and belly of females were white, but our one female (fig. 15) has the throat brown and the belly is heavily suffused with brown.

REMARKS: Heyer (1979) summarized variation in adult *Leptodactylus rugosus*, but his treatment includes a sibling species and he is in the process of reanalyzing the variation and taxonomy. Our sample, as verified by Heyer (personal commun.), seems to be conspecific with the holotype of *rugosus*.

With two exceptions, the 11 males in this sample have cornified thumb and chest spines; the exceptions (41 and 50 mm SVL) lack chest spines and the thumb spines are not cornified. Thus, in this sample sexual maturity in males seems to be approached starting at about 41 mm (table 5).[8] There is one spine on each thumb (fig. 15, middle) and a pair of tiny pectoral spines on each side (a single tiny spine on right side of male in fig. 15). All the Guaiquinima specimens have tubercles on the tibia and tarsus and most have a few tubercles on the foot.

LIZARDS

FAMILY POLYCHRIDAE (FORMERLY ANOLOID IGUANIDAE)

Anolis chrysolepis planiceps Troschel

Anolis planiceps Troschel, 1848: 649–650. Type locality, "Caracas."

MATERIAL: AMNH 136151, Summit Camp 1.

NATURAL HISTORY: The specimen, an adult female, was captured in the tall forest south of Camp 1; a male from the same place escaped; a third individual was seen in the scrubby savanna adjacent to Camp 1. The female is 69 mm SVL, with a tail of 141 mm. It has 13/14 supralabials; supralabial 10/11 under center of eye; 11/12 infralabials; 7/5 canthals; 7/7 loreals/ 2/2 subocular rows; 159 scales around midbody; 46 rows of ventrals from the anterior margin of the arm to midthigh; 15/15 expanded subdigital lamellae under finger IV; 9/8 terminal subdigital lamellae under finger IV; 25/26 expanded subdigital lamellae under toe IV; 8/8 terminal subdigital lamellae under toe IV.

COLOR PATTERN: In life, light yellowish brown with a dark interorbital bar and ill-defined blackish brown markings on the flanks and limbs; paired dark brown sacral spots; ventral surfaces white with brown under the tail and limbs. Iris greenish bronze above, suffused with black on each side and below. Tongue pale orange, throat lining unpigmented. The small dewlap was dull orange with grayish white scales; the male that escaped had a darker and brighter orange-red

[8] In the original description of *L. rugosus*, Noble (1923: 297) erred in stating that the holotype is "an adult male" and that males lack nuptial spines. The holotype (AMNH 1169, 38 mm SVL) is immature.

dewlap. These dewlaps seem closest to those attributed to the subspecies *planiceps*, which has a "uniformly red" or "reddish" dewlap with white scales (Vanzolini and Williams, 1970: 78, 86).

Anolis fuscoauratus d'Orbigny

Anolis fusco-auratus d'Orbigny *in* Duméril and Bibron, 1837, 4: 110–111. Type locality "Chile" in error, probably Bolivia (see Peters and Donoso-Barros, 1970: 53, for references).

MATERIAL: AMNH 136152, Summit Camp 1.

NATURAL HISTORY: A sleeping specimen was found in the tall forest south of Camp 1; it was lying horizontally on a leaf about 1 m aboveground. The specimen is a female 49 mm SVL, 90 mm tail length. It has 8/9 supralabials; supralabial 7/8 under center of eye; 9/10 infralabials; 8/8 canthals; 6/6 loreals; 1 row suboculars; 2 scale rows between supraocular semicircles; 95 ventrals; 153 scale rows around midbody; 16/15 expanded subdigital lamellae under finger IV; 7/7 terminal subdigital lamellae under finger IV; 28/28 expanded subdigital lamellae under toe 14; 9/9 terminal subdigital lamellae under toe IV.

COLOR PATTERN: In life, the dorsum was olive-brown with five black middorsal blotches, and black interorbital bar and head mottling; ventral surfaces white with brown speckling and suffusion. The vestigial (female) dewlap was white with gray scales. Iris was orange-bronze becoming brown posteriorly. Tongue was pale pink; throat lining unpigmented.

In preservative, body brown and interorbital bar reddish, other markings remaining black. Tail with a black medial stripe along its anterior third, black bars posteriorly. Distinct pale spots on ventral surfaces of thighs and tail near the base; indistinct light areas on posterior surface of thigh.

The color pattern in preservative agrees with one of the two female pattern types described for *A. f. kugleri* in Surinam (Hoogmoed, 1973: 134). The description of squamation also agrees with that of Hoogmoed, except that AMNH 136152 has two rows of scales between the supraocular semicircles. (According to Peters and Donoso-Barros (1970), the two subspecies of *A. fuscoauratus* differ in this character, with *A. f. fuscoauratus* having two or more scale rows between the semicircles and with *A. f. kugleri* having one row.) See Hoogmoed (loc. cit.) for a discussion of the geographic range of *Anolis f. kugleri* Roux, which originally was described as a Venezuelan species.

FAMILY TROPIDURIDAE (FORMERLY TROPIDURINE IGUANIDAE)

Plica lumaria, new species

Figures 16–19, 20B

HOLOTYPE: AMNH 136176 (field no. CWM 18976), an adult male collected by C. W. Myers and M. A. Donnelly on February 24, 1990, at approximately 1090 m elevation, Cerro Guaiquinima, Bolívar, Venezuela.

PARATOPOTYPES: A total of 13 specimens (3♂, 5♀, 5 juv.) as follows: AMNH 136177–136189, from 1060–1090 m elevation at the type locality, collected February 25–March 1, 1990, by M. A. Donnelly and C. W. Myers.

ETYMOLOGY: The species name is a Latin adjective (of thorns) referring to the thornlike scales that cover the body.

DIAGNOSIS: A *Plica* (fig. 16) having a complete antegular fold overlapping or slightly anterior to a complete gular fold; a deep ventral mite pocket (ventral to antegular fold) at lateral extent of gular fold that is continuous with deep pocket in the antehumeral fold; a well-developed middorsal crest on body and tail; small, slightly imbricate, acutely pointed, thornlike scales covering dorsal and dorsolateral surfaces of body and limbs; differentiated dorsolateral and ventrolateral rows of enlarged acutely pointed scales; distinctive tufts of spines on sides of neck; reduced preauricular fringe with enlarged scales pointed laterally; 3–4 rows of scales between suboculars and supralabials.

Plica lumaria differs from both of its congeners in being black with small yellowish spots (dorsal ground color basically green in *P. plica* and *P. umbra*). *Plica umbra* differs from the larger *P. lumaria* and *P. plica* in lacking spiny tufts on the neck, in a less depressed body, and in having larger head shields and body scales. *Plica lumaria* most resembles *P. plica* in general habitus but differs in many aspects of scalation, including laterally directed superciliary scales (dorsally directed in *P. plica)* and in body scales mostly

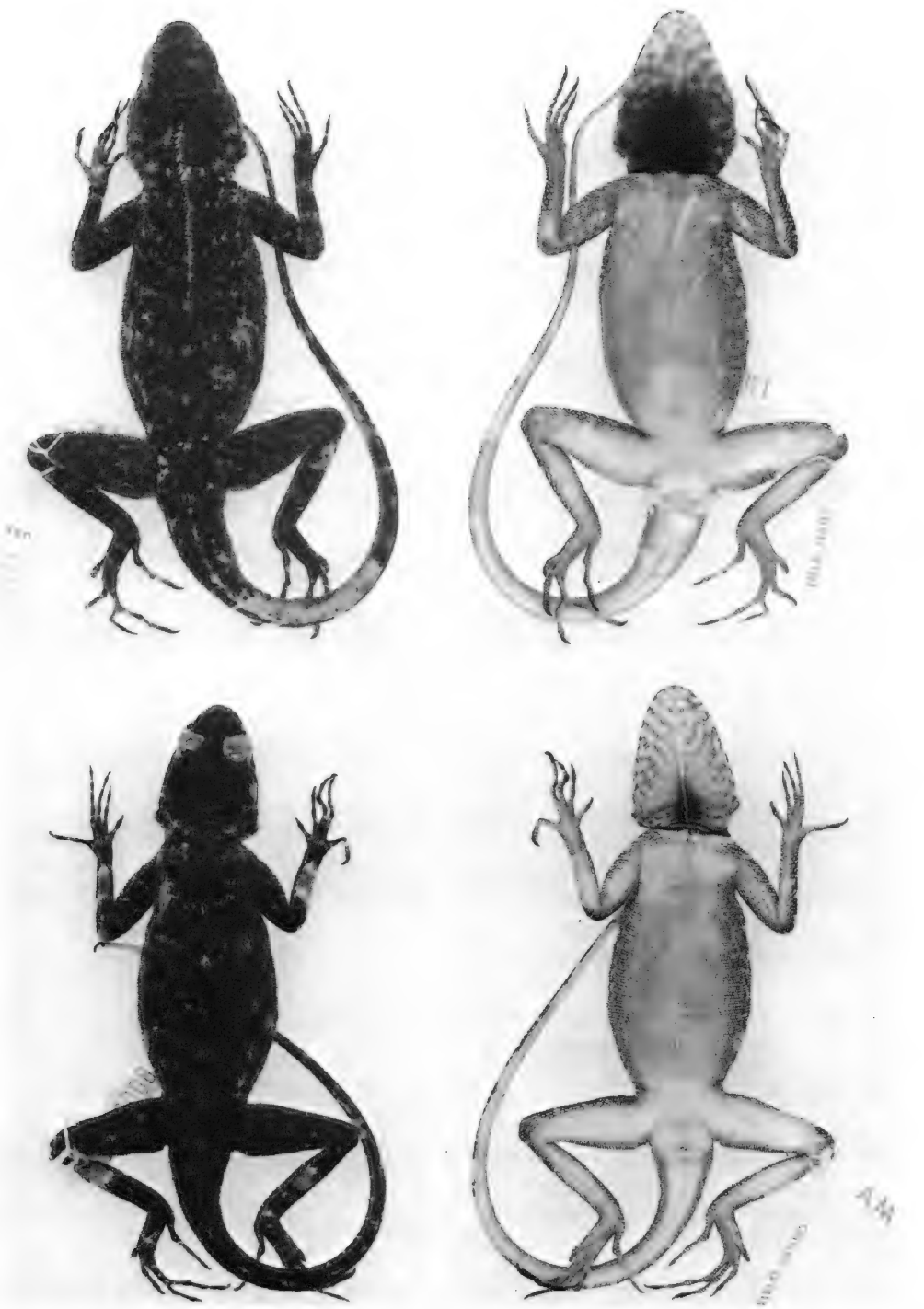

Fig. 16. *Plica lumaria*, n. sp., dorsal and ventral views of adult male (AMNH 136176, holotype) and adult female (AMNH 136189, paratopotype). Top, ♂ ×0.67. Bottom, ♀ ×0.80.

acutely pointed or thornlike (slightly pointed or keeled in *P. plica)*. See Comparisons with Spiny-Necked Tropidurines for additional discussion.

Body Size and Proportions

Head large, head length (measured obliquely from tip of snout to angle of jaw)

27–30 percent of SVL; head longer than wide and wider than high; wider than neck; neck narrower than body. Snout broadly rounded in dorsal view, slightly convex in profile, not projecting over mouth. Body wider than deep. Limbs long and slender; pentadactyl; relative finger and toe lengths, I < V < II < III < IV. Tail 1.5–1.8 times SVL; in males, tail width at base subequal or equal to tail depth; in females and juveniles, basal tail width > depth; tail compressed posteriorly, becoming round at end. Four adult males with maximum SVL of 100 mm (76–100 mm, $\bar{x}$ = 88.5 mm, *S.D.* = 10.97. Five adult females with maximum SVL of 78.5 mm (76–79 mm, $\bar{x}$ = 77.1, *S.D.* = 1.19). Largest of five undissected juveniles 71 mm SVL (54–71 mm, $\bar{x}$ = 64.3, *S.D.* = 6.24).

Description of Scalation

Head (fig. 17): Dorsal surface anterior to large interparietal covered by moderate-size smooth scales. Interparietal roughly triangular, wider than long; in contact with small pointed scales posteriorly, lateral margins in contact with irregularly shaped smooth scales. Scales of frontonasal region (anterior margin interparietal to posterior margin nasals) irregularly shaped, smooth; imbricate anteriorly; in 2–3 rows between circumorbital series. Circumorbitals in 2–3 rows; innermost row largest, with anterior and posterior scales resembling supraoculars in being longer than wide. Supraoculars 2–3.[9] Superciliary scales longer than high, in three stacked rows; scales in middle row largest; superciliaries forming a laterally projecting crest that extends beyond orbit.

Nasals separated from rostral and first supralabial by one row of scales dorsal to supralabials. Internasals 11–19 in 3–4 rows (holotype, 12 scales in 3 rows); anteriormost row in contact anteriorly with scale row that separates nasal from rostral. Superciliary series terminates in one canthal scale; canthal in contact either with nasal or postnasal (canthal-nasal contact in 8 specimens, canthal-postnasal contact in 3, and bilaterally asymmetric in 3, including holotype). Loreal region with 7–16 moderate-size, irregularly shaped smooth scales (holotype, 8 scales). No distinct prefrontal. Median suboculars 1–5 (no. median suboculars bilaterally symmetric in 3 specimens, including holotype [3/3]; asymmetric in 8 specimens, with counts of 1/4, 2/4, 3/4, 3/5, and 5/4). Posterior suboculars 1–2 (holotype, 2). Temporal region with moderate-size granular scales, which imbricate anteriorly. Rostral wider than high, as high as adjacent supralabial. Supralabials 4/4 (5/4 in one).

Mental scale extending slightly posteriorly or not beyond anterior margins of infralabials; paired postmental series distinguishable or not. Infralabials 4–6 (4/5 in one, 5/5 in eight, including holotype, and 6/5 or 5/6 in five). Gular scales smooth; lateral gulars laterally imbricate, median gulars posteriorly imbricate. Acutely pointed scales at angle of jaw.

Tympanum: Ear canal deep. Three rows enlarged scales bordering anterior and dorsal margins of canal, these enlarged scales pointing mostly laterally. Small, conical scales lining ventral margin of canal and a cluster of enlarged, pointed scales at anteroventral margin; posterior rim with small conical scales, increasing in size dorsally.

Neck (fig. 17): Dorsal surface with small, slightly imbricate, acutely pointed scales on either side of enlarged median crest (see under Body below).

Dorsolateral neck surface with an area of enlarged thorny scales (3–6 scales above posterodorsal rim of ear canal) and two distinctive tufts of spines. Larger spiny tuft lying dorsal to oblique neck fold; smaller tuft lying six rows posterior to largest tuft, above level of anterior margin of arm.

Lateral neck surface with small pointed or conical scales, slightly imbricate and smaller than scales on dorsal surface. Two tufts of laterally directed spines at posteroventral margin of ear canal. Anteriormost tuft larger and slightly ventral to posterior tuft; tufts connected by a single pointed scale. Small pointed scales on ventral surface of neck. Scales of antegular mite pockets long, acutely pointed.

[9] Number of rows of circumorbitals and number of supraocular scales variable as follows: 3 rows circumorbitals and 3 supraoculars (N = 4 specimens); 2 rows circumorbitals and 3 supraoculars (N = 3, including holotype); 3 rows circumorbitals and 2 supraoculars (N = 1). Six other individuals show bilateral asymmetry: 2 rows circumorbitals and 2 or 3 supraoculars (N = 3); 3 rows circumorbitals and 2 or 3 supraoculars (N = 3).

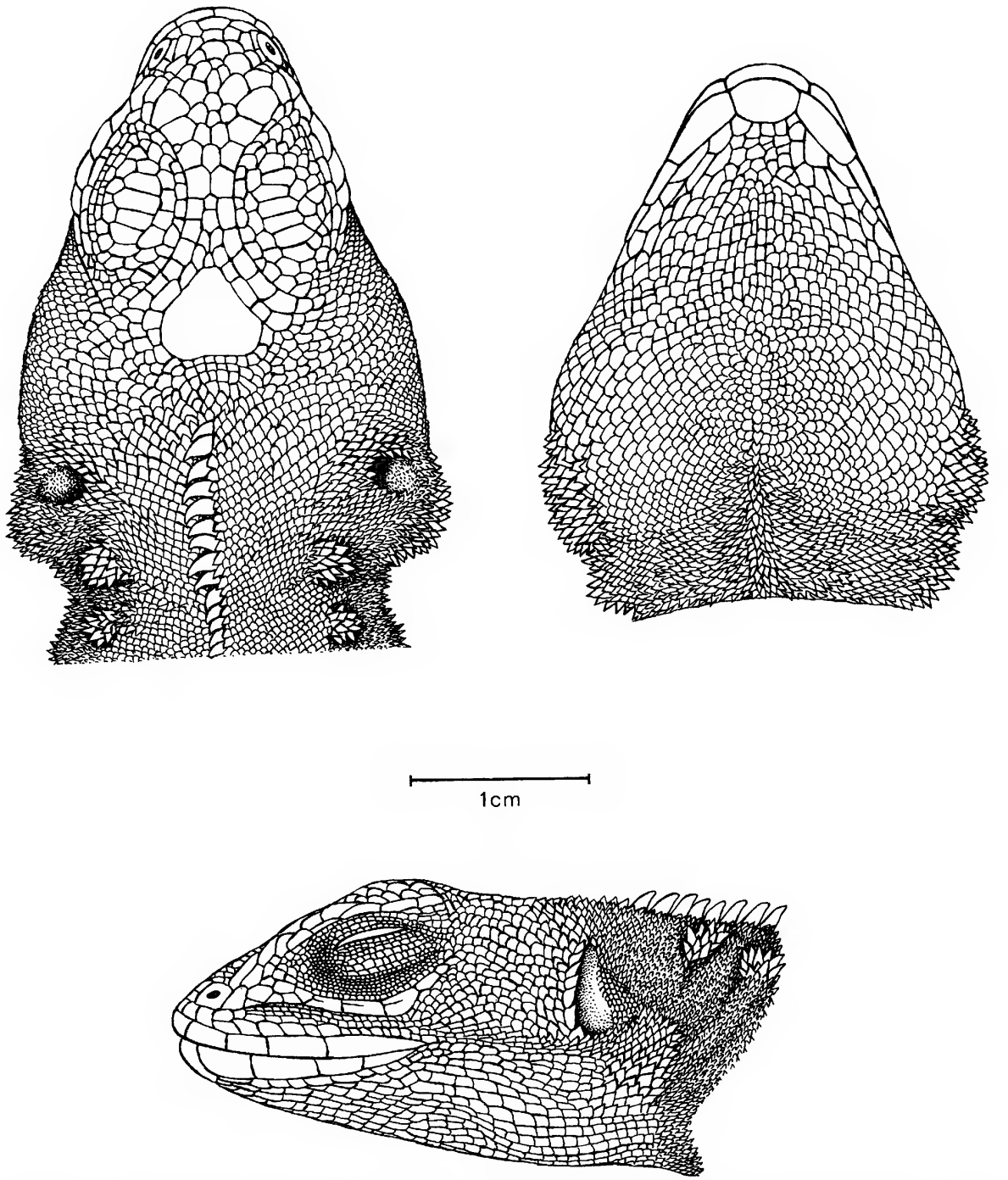

Fig. 17. *Plica lumaria*, n. sp. Dorsal, ventral, and lateral views of head of AMNH 136176 (♂ holotype); ×2.6. *Patricia J. Wynne.*

POCKETS AND FOLDS:[10] Antegular fold complete, slightly anterior to or overlapping gular fold. Deep anteriorly directed pockets in lateral portions of antegular fold (medial to angle of jaw). Oblique neck fold present; scales lining fold not reduced in size. Gular fold complete medially; large ventral pocket

[10] Terminology of the "mite pockets" and folds follows Frost (MS).

continuous with lateral pocket in antehumeral fold; gular pocket ventral to antegular pocket). Rictal fold present. Dorsolateral fold present, continuous laterally with antehumeral fold, extending to posterior margin of arm; scales on outer surface of fold elongate. No axillary pocket. No groin pocket.

BODY: A middorsal crest of laterally compressed, long pointed scales directed dorsally. Crest beginning 3–6 rows behind interparietal and continuing onto tail, with total of 72—86 scales (74 in holotype). Middorsal crest present in all specimens, being most well developed in mature males and most poorly developed in smallest juvenile.

First scale in crest generally the smallest, with crest scales increasing in height posteriorly to a maximum height at scale 4 (N = 4, including holotype), scale 6 (2), scale 7 (5), or scale 8 (1); crest scales 1–11 are equal in one specimen (AMNH 136188). Scale height decreases posterior to tallest crest scale. Lateral width of crest scales 1.5–2 times the length of adjacent paravertebral scales, increasing from head to maximum at midbody, then decreasing posteriorly.

Body to either side of middorsal crest with slightly imbricate, acutely pointed scales, pointing dorsally or posterodorsally. Paravertebral scales (from posterior margin interparietal to level of posterior margin of thigh) in 137–157 rows ($\bar{x}$ = 146.4, $S.D.$ = 6.54; holotype, 157). Three or four dorsolateral rows of enlarged, pointed scales, continuous anteriorly with dorsolateral fold. Three or four rows of enlarged pointed ventrolateral scales from axilla to groin. Enlarged dorsolaterals larger than enlarged ventrolaterals; scales in both rows larger than adjacent body scales. Scales around midbody in 141–156 rows ($\bar{x}$ = 146.2, $S.D.$ = 2.58; holotype, 151).

Venter with smooth scales, in 35–39 rows across chest ($\bar{x}$ = 37.2, $S.D.$ = 0.98; holotype 37 rows) and in 92–117 rows from gular fold to vent ($\bar{x}$ = 103.9, $S.D.$ = 5.74; holotype, 117).

ARMS AND LEGS: Dorsal surface of upper arm with slightly imbricate, acutely pointed scales projecting dorsally or laterally. Upper arm scales larger than those on adjacent body. Dorsal surface of lower arm with imbricate, mucronate scales. Elbow scales smooth. Posterodorsal surface upper arm with pointed scales; posteroventral surface of upper arm with smooth, mucronate scales, becoming pointed distal to elbow. Anterior surface of upper arm with acutely pointed scales, becoming smooth and imbricate distal to elbow. Ventral surface with smooth scales. Smooth scales (some slightly mucronate) on top of hand, weakly keeled scales on palm. Subdigital lamellae bicarinate or tricarinate. Subdigital lamellae of fourth finger 20–24 (holotype 22/21).

Dorsal thigh with slightly imbricate, pointed scales larger than those of adjacent body; imbricate, mucronate scales on anterior thigh surface, slightly imbricate, pointed scales on posterior surface. Knee scales smooth; scales keeled, imbricate, and mucronate on lower leg. Ventral surface with smooth scales, decreasing in size toward anterior and posterior sides. Dorsal scales of foot proximally small, mucronate, imbricate; distally keeled, mucronate, imbricate. Sole of foot with keeled, mucronate, imbricate scales. Subdigital lamellae bicarinate or tricarinate; 27–33 lamellae under toe 4 (holotype, 30/31).

TAIL: Middorsal scale row enlarged, continuous with middorsal body crest, distinct on anterior third of tail. Dorsal side of basal part of tail with mucronate, juxtaposed scales, posteriorly becoming keeled, mucronate, and imbricate. Scales on side of tail pointed and juxtaposed, posteriorly becoming weakly keeled, mucronate and imbricate. Subcaudals smooth, imbricate, slightly mucronate.

COLORATION

Field Notes for AMNH 136176–136181: In life, the dorsal surfaces of head, body, and limbs were black with small yellowish tan spots and flecks. Pale areas over the eyes and labials varied from tan in smaller lizards to light orange in adults. Chin with a faint to strong wash of orange. Throat black, rest of ventral surfaces pale brown. Adult males with golden yellow patches on abdomen, precloacal area, and thighs.

VARIATION IN TYPE SERIES: Black ground color retained in preservative—except becoming gray as patches of stratum corneum fall away due to handling. Interparietal with small, rounded yellow or tan spots. Small yellowish spots on head, body, limbs, and tail frequently coalesced to form ill-defined transverse bars or rows of spots (head, 0–3

bars; body posterior to nuchal collar, 2–7 bars). Distinct black nuchal collar 9–10 scales wide, bordered anteriorly and posteriorly in most specimens by ill-defined yellow bars 2–3 scales wide (yellow bars represented by spots in holotype, broken or indistinct in a few specimens and absent in one). Yellow bars on forearm and hand present in all; bars distinct on the hind limbs of a few. Yellow bars discernible on tail of all but the smallest juvenile.

Venter beige or dirty white, posteriorly with yellow (♂) or pink (♀) wash in adults. Underside of head mottled gray and white anteriorly, except that holotype has an orange wash anterior to the black throat. Usually a median white line discernible under head, extending from rear edge of mental to the gular fold; this marking virtually absent in holotype (fig. 16). A variably sized black spot or patch on throat in front of gular fold (fig. 16, table 6).

SEXUAL DIMORPHISM: Adult males have golden yellow patches on posterior belly, precloacal area, and underside of thighs. Black pigmentation on the throat is extensive in males (fig. 16, table 6). Adult females lack the ventral patches of golden yellow, but have instead a pink wash in the same areas; the black throat spot is small in females (fig. 16, table 6).

Five undissected lizards were classified as juveniles based on size (< 72 mm SVL), although we are fairly confident that we can determine sex of the four largest because of color pattern and throat spot size (table 6): One specimen (136180) is probably an immature male; the thighs and precloacal area are yellow, and the throat spot is intermediate in size. Three others are probably female because there is some pink on the venter and the throat spots are small. The smallest juvenile has a white venter and a small spot.

TABLE 6
Variation in Throat Spot Size in Type Series of *Plica lumaria*, new species[a]

AMNH	Sex	Spot length	Spot width	CSL	CSW	Area
136176	♂	19.1	16.7	0.685	0.745	0.510
136177	♂	19.2	15.3	0.651	0.686	0.447
136178	♂	15.2	7.5	0.601	0.389	0.234
136179	♂	12.0	9.0	0.533	0.804	0.429
136182	♀	7.2	2.8	0.285	0.171	0.049
136183	♀	7.2	3.0	0.308	0.183	0.056
136186	♀	5.0	3.8	0.215	0.220	0.047
136187	♀	7.5	3.0	0.333	0.182	0.061
136189	♀	7.0	4.3	0.300	0.259	0.078
136180	I♂	7.0	8.0	0.342	0.520	0.178
136181	I♀	5.5	3.5	0.312	0.247	0.077
136185	I♀	4.3	1.9	0.223	0.142	0.032
136188	I♀	4.2	2.5	0.214	0.174	0.037
136184	J	6.0	2.8	0.403	0.244	0.098

[a]Abbreviations: CSL, spot length/head length; CSW, spot width/head width; Area = CSL x CSW; I♂ or I♀, sexually immature; J, unsexed juvenile.

HEMIPENES

The spineless hemipenes are tiny; the right organ of the holotype (100 mm SVL) has a length of < 9 mm from its base to the tip of a lobe. The hemipenis is divided for nearly half its length (fig. 18). The sulcus sperma-

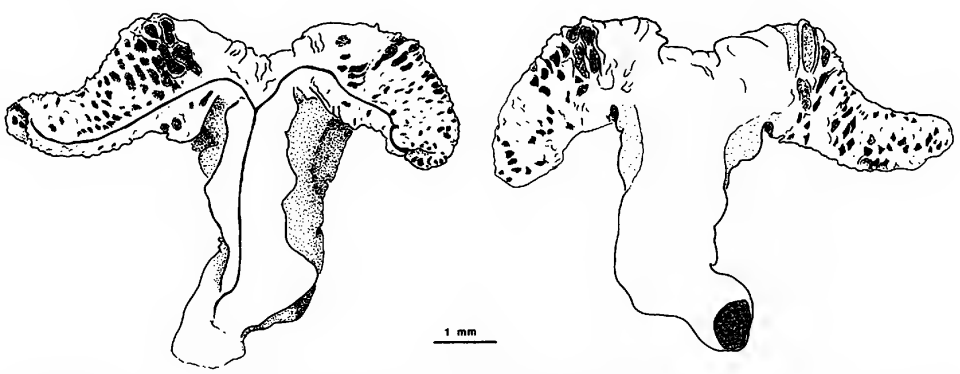

Fig. 18. Hemipenis of *Plica lumaria*, n. sp. Right organ of AMNH 136176 (holotype).

Fig. 19. Type locality of *Plica lumaria*, new species.

ticus bifurcates just proximal to the crotch and the sulcus branches extend centrolineally nearly to the tip of each lobe. The undivided basal part of the organ lacks ornamentation; lateral alae develop midway up the stalk and terminate on the asulcate base of each lobe. The distal 70 percent of each lobe is calyculate, the calyces decreasing in size distally from the first several large basal calyces. The calyculate regions are not joined in the crotch, which is nude.

Habitat and Natural History

The holotype and paratypes were collected at 1060–1090 m elevation along the north stream a few km northwest of Summit Camp 1 (fig. 19); none was seen in similar habitat in the immediate vicinity of Camp 1 (1030 m) nor in the nearly streamless savanna at Camp 2 (1150 m). Their distribution on Cerro Guaiquinima may be spotty, although this species can be easily overlooked. All our specimens were taken from rocks and boulders in and along the stream bed or along rock faces on either side of the stream.

Plica lumaria is diurnal and is active on both sunny and overcast days. Specimens were collected in the afternoon when they were perched on rocks either in direct sun or in shaded areas (fig. 20B). These lizards were very shy, running into deep crevices or under rock ledges when disturbed. Head-bobbing was observed.

On February 28, five animals were collected in an overcast afternoon with periods of light rainfall. Body temperature was taken with a quick-reading thermometer inserted into the cloaca immediately after they were shot; they were not handled during this process and the rock temperature was recorded after cloacal temperature. Body temperature exceeded rock temperature (table 7), with a mean difference of 2.5°C.

Stomach contents were removed from two adult females. Both stomachs contained ants (30 ants representing 12 morphospecies), and 17 small bees were in one. In addition to the

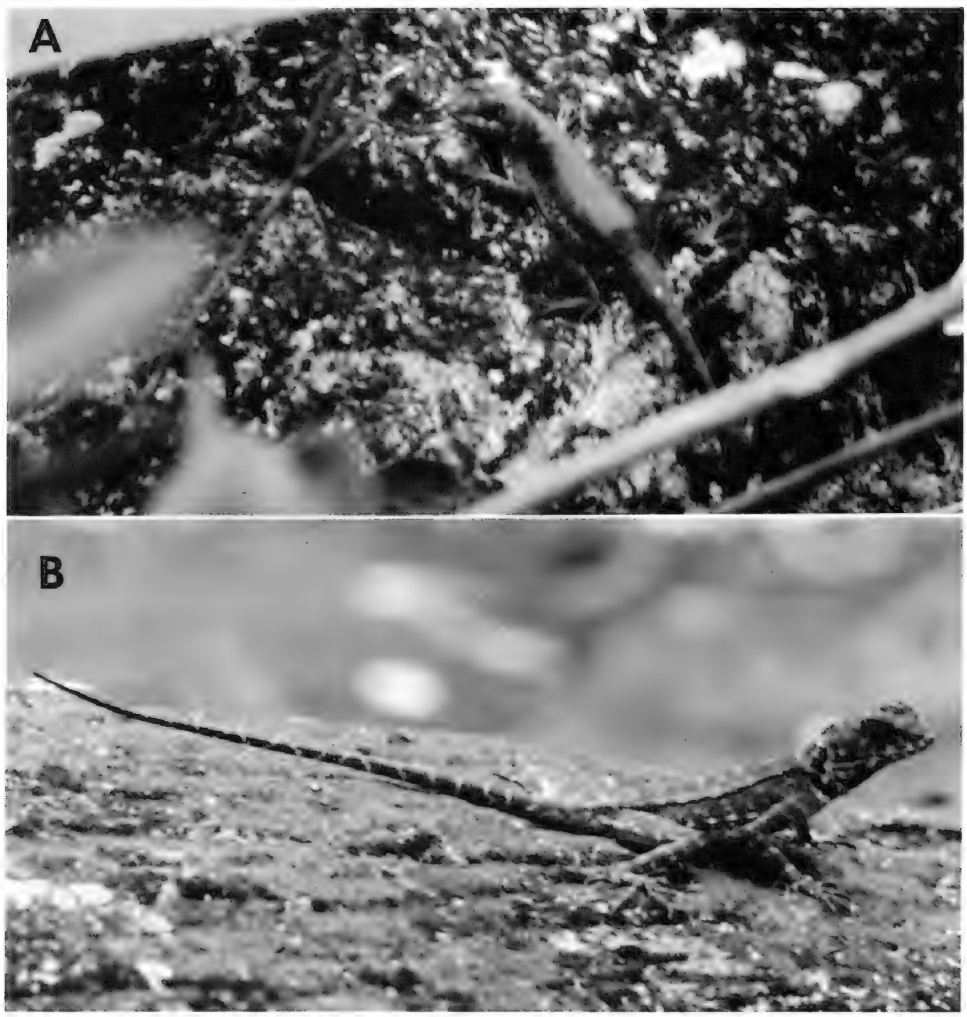

Fig. 20. Cerro Guaiquinima tropidurines in life (photographed near Summit Camp 1). **A.** *Tropidurus hispidus* (Spix), a geographically widespread species. **B.** *Plica lumaria*, an apparent endemic.

Hymenoptera, a small scorpion was taken from one gut and a beetle larva was removed from the other.

Comparisons with Spiny-Necked Tropidurines

In addition to *Plica lumaria*, the following eight members of the monophyletic *Tropidurus* group (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989) also have tufts of enlarged spines on the neck according to Frost (MS):

Plica plica
Strobilurus torquatus
Tapinurus spp. (3)

TABLE 7
Cloacal Temperatures of *Plica lumaria*, New Species
(T_C = cloacal temperature; T_R = rock surface temperature)

AMNH	Time (h)	T_C (°C)	T_R (°C)	$T_C - T_R$ (°C)
136184	1246	29.5	27.0	2.5
136185	1315	34.4	32.2	2.2
136186	1410	31.2	28.6	2.6
136187	1418	28.6	24.2	4.4
136188	1452	29.4	28.6	0.8

Tropidurus bogerti
Tropidurus mucujensis
Tropidurus spinulosus

Strobilurus torquatus (AMNH 120472) differs from the other spiny-necked tropidurines in tail size and squamation. The tail is subequal to SVL and bears large, strongly mucronate scales.

Tapinurus semitaeniatus (AMNH 131864–131866) differs from *Plica lumaria* in the following characters: It lacks a middorsal crest and differentiated dorsolateral and ventrolateral scale rows (although there is a distinct dorsolateral fold); the body is covered with smooth, juxtaposed scales that decrease in size laterally; it has a single row of scales between the subocular series and supralabials; it has a single large median subocular; it has incomplete gular and antegular folds; the rostral is taller than adjacent supralabials; it has 8/8 infralabials. The small specimens (SVL < 70 mm) of *semitaeniatus* that we examined lack neck spines, but adults develop distinct tufts of spines (D. R. Frost, personal commun.).

A color pattern of vague pale cross-lines on a dark ground is shared between *Plica lumaria* of Cerro Guaiquinima and a neighboring tepui endemic, *T. bogerti* of Auyantepui (Roze, 1958a). The similarity in color pattern between these geographic neighbors might owe itself to adaptive responses to similar environments or to some other reason, but morphological differences seem to argue against a close (sister-group) relationship. *Tropidurus bogerti* (AMNH 61012, 61014–61015, 61017, USNM-RWM 11643–11645, 11655, 11657) lacks pockets in the gular fold; the gular fold is incomplete medially; the antegular pockets are lateral to the angle of the jaw; there is no middorsal crest; mature males have black spots on the undersides of the thighs; and the lateral gular scales are not imbricate.

Tropidurus mucujensis (MCZ 172944, 172945), a black, rock-dwelling species, lacks a middorsal crest on the body and tail; lacks dorsolateral and ventrolateral body folds; lacks antegular and gular folds; has elongate, posteriorly directed preauricular fringe scales; the head shields (anterior to parietal) are not imbricate; the scales on the dorsal and lateral body surfaces are keeled and mucronate; the limbs are stocky; the spots on the undersides of the thighs and the precloacal area are black.

Tropidurus spinulosus (AMNH 101489, 101491, 101493, 101496) has an incomplete gular fold; has a large single median subocular; has the rostral higher than adjacent supralabials; lacks differentiated dorsolateral and ventrolateral scale rows; dorsal and lateral body scales are keeled; the scales of the preauricular fringe point posteriorly; and the superciliary crest barely extends laterally beyond the orbit.

Plica lumaria most closely resembles *Plica plica* (AMNH 36629, 36640, 36650, 36662, 107590, USNM-RWM 17127, 17407, 17620, 17635, 17684, 17689, 17740). Both species have long, thin limbs, middorsal crests, differentiated dorsolateral and ventrolateral rows of enlarged scales, fragmented suboculars, 3–5 scale rows between suboculars and supralabials, small scales covering the body, mite pockets in the gular and antegular folds, and posterior throat spots. Body scale morphology differs between the two species—in *P. lumaria*, the majority of body scales are acutely pointed, whereas in *P. plica* they are slightly pointed or keeled. Shape, size, and arrangement of the superciliaries also differ: The superciliaries are higher than long in *Plica plica* but longer than high in *P. lumaria;* they form a dorsally directed crest in *P. plica*, whereas the crest points laterally in *P. lumaria*. The scales on the occipital region of the head (posterior and lateral to the interparietal) are large and keeled in *P. plica*, small and pointed in *P. lumaria*. The color patterns are different: *P. plica* is green with brown bands on body and limbs (Etheridge, 1970; Hoogmoed, 1973), whereas *P. lumaria* is black with narrower, less distinct yellowish tan bands.

Certain characters (e.g., larger prefrontal scales, narrower head) argue for *P. lumaria* being the plesiomorphic sister taxon of *P. plica* rather than a peripheral isolate of that species (D. R. Frost, personal commun.).

Plica lumaria appears to be a rock dweller and *P. plica* normally is found on tree trunks. But the latter species has been observed occasionally on large boulders in Surinam (Hoogmoed, 1973) and on both rocks and trees at 600 m on Cerro Yapacana in Ama-

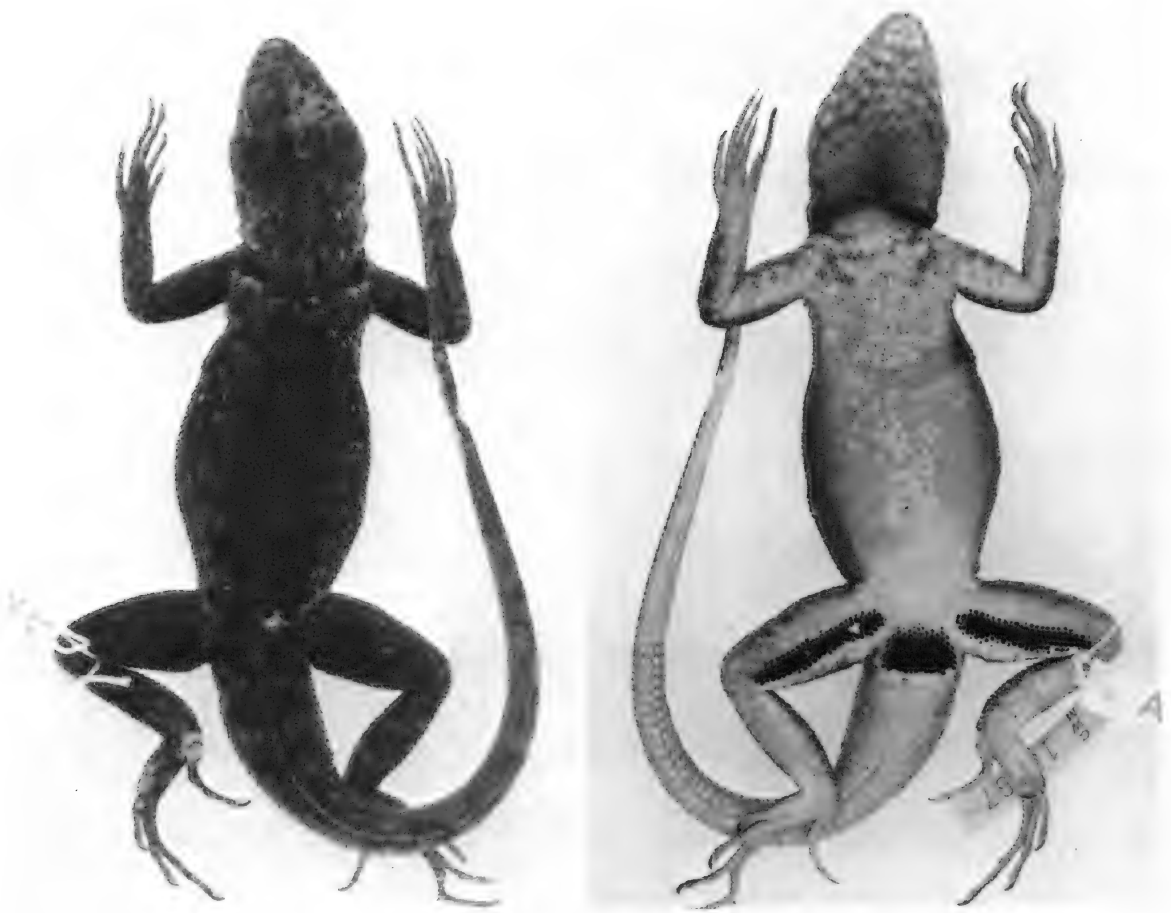

Fig. 21. *Tropidurus hispidus* (AMNH 136168, ad. ♂), in dorsal and ventral view, ×1.

zonas, Venezuela (Myers, personal obs.). All three species of *Plica* feed on ants and may prove to be ant specialists.

Tropidurus hispidus (Spix)

Figures 20A, 21

Agama hispida Spix, 1825: 12, pl. 15, fig. 2. Syntypes from Bahia or Rio de Janeiro, Brazil (described jointly with *A. tuberculata* on p. 12, pl. 15, fig. 1); lectotype designated by Hoogmoed and Gruber (1983: 387), probably from Bahia (restricted to Salvador, Bahia by Rodrigues, 1987: 175).

MATERIAL: AMNH 136164–136175, Summit Camp 1; AMNH 136153–136163, Summit Camp 2.

NATURAL HISTORY: *Tropidurus hispidus* was the most common lizard at both camps. At Camp 2 (1150 m) it was found on rocks in the open savanna and along stream beds; at Camp 1 it was found on rocks adjacent to the open stream north and east of camp. All lizards collected at Camp 1 were in open habitats below 1060 m, whereas *Plica lumaria* was found at 1060–1090 m. Sympatry between *Plica* and *Tropidurus* was expected but not observed at our sites.

On Cerro Guaiquinima, *T. hispidus* is diurnal; all were captured between 0900 and 1800 h. They were seen adpressed to rocks and basking in the morning and were active until dusk, this observation being consistent with that made by Myers and Daly in Surinam (in Hoogmoed, 1973: 190). Two were shot at midday and cloacal and substrate temperatures were taken immediately with a quick-reading thermometer. One lizard had a body temperature of 35.2°C at a substrate temperature of 30.8°C at 1200 h; the second

TABLE 8
Size (in mm) and Scale Counts for *Tropidurus hispidus* from Cerro Guaiquinima
(Values are means ± 1 SD, with ranges in parentheses)

Character	Males (N = 10)	Females (N = 9)	Juveniles (N = 4)
Snout-vent length	79.40 ± 5.50 (68.0—86.0)	65.72 ± 2.97 (61.0—70.0)	43.00 ± 5.79 (37.5—51.0)
Tail length	110.78 ± 12.60 (95.0—124.0)	89.40 ± 8.08[b] (83.0—103.0)	67.50 ± 9.76[c] (57.5—77.0)
Tail length/SVL	1.38 ± 0.20 (1.07—1.66)	1.35 ± 0.11[b] (1.25—1.47)	1.54 ± 0.04[c] (1.51—1.58)
Dorsal scale rows[a]	75.0 ± 2.79 (70—78)	76.8 ± 4.06 (71—82)	71.0 ± 3.83 (68—76)
Scales around midbody	69.7 ± 2.67 (66—74)	73.9 ± 1.90 (71—77)	72.3 ± 2.22 (69—74)
Transverse ventrals	89.6 ± 4.77 (80—97)	85.2 ± 5.24 (78—92)	88.3 ± 0.58 (88—83)
Subdigital lamellae finger IV	18.5 ± 0.96[d] (17—21)	17.9 ± 0.68[e] (17—19)	17.2 ± 1.47[f] (16—19)
Subdigital lamellae toe IV	25.8 ± 1.71[g] (22—28)	26.4 ± 0.63[e] (25—27)	24.8 ± 1.28[h] (23—27)
Supralabials	6.1 ± 0.24[i] (6—7)	5.9 ± 0.32[i] (5—6)	5.8 ± 0.46[h] (5—6)
Infralabials	6.3 ± 0.45[d] (6—7)	6.0 ± 0.49[i] (6—7)	5.5 ± 0.54[h] (5—6)

[a] Dorsal rows from occiput to rump.
N = [b] 9, [c] 5, [d] 19, [e] 16, [f] 6, [g] 20, [h] 8, [i] 18.

had an identical body temperature of 35.2°C at a substrate temperature of 29.8°C at 1236 h. The differences between cloacal and substrate temperatures are higher than the average difference of 2.5°C found in a sample of *Plica lumaria* (table 7).

COLOR PATTERN: In life, dark brown with lateral black nuchal marks forming an incomplete or occasionally complete collar that is pale-bordered in males. Underside of head dark mottled, remaining mottled or becoming overall blackish on the throat (fig. 21), sometimes with a discrete small gular spot. Venter and undersides of limbs pale, slightly bronzy pink in life, with males having black markings on the undersides of the thighs and precloacal area (fig. 21); two males also with some black spotting on the abdomen (contra Rodrigues, 1987: 175).

REMARKS: *Tropidurus hispidus* has been considered a subspecies of *T. torquatus* (Burt and Burt, 1931; Roze, 1958a; Hoogmoed, 1973) until recently (Rodrigues, 1987). *Tropidurus hispidus* has a single axillary mite pocket, whereas *T. torquatus* has 2–3 depressions behind the arm that are lined with granular scales (Rodrigues, 1987).

Coloration of Guaiquinima *T. hispidus* in life differs in minor respects from descriptions of Surinam specimens by Hoogmoed (1973: 189), who described the venter as white and juveniles as having bluish throats with lighter dots. In squamation, the Guaiquinima specimens resemble those described by Hoogmoed (1973) and Rodrigues (1987). All have a single row of scales between the subocular and supralabials, one subocular, and one preocular. Variation in size and scale counts are summarized in table 8.

FAMILY TEIIDAE

Ameiva ameiva (Linnaeus)

Lacerta ameiva Linnaeus, 1758: 202. Type locality, "Habitat in America."

MATERIAL: AMNH 136192–136194, Summit Camp 1; AMNH 136190—136191, Summit Camp 2.

Ameiva ameiva occurred sparsely in dense savanna vegetation surrounding both camps, where these lizards seemed to frequent vegetated areas and to avoid open rocky places. One was also seen at Camp 1 in a sun fleck in the forest edge along south stream. *Ameiva* was much less common at our camps than either *Tropidurus* or *Plica*.

The Guaiquinima specimens have 4/4 supraoculars, 1/1 loreals, one row of scales between the superciliaries and supraoculars, 1/1 preoculars, suboculars 3/3 (one specimen has first subocular on right fused with prefrontal), and 10 longitudinal ventral rows (at ventral 15). Variable counts include: 6–8 supralabials, 5–7 infralabials, 6–7 superciliaries, 4–5 pairs of chin shields, 3–5 palpebrals in the lower eyelid, 4–5 terminal preanals, 35–44 femoral pores, 29–30 transverse ventral rows, 139–154 granules around the body at ventral 15, 13–15 subdigital lamellae under finger IV, 30–40 subdigital lamellae under toe IV, 37–41 scales around the tail at

verticil 15. The squamation agrees with the description provided by Hoogmoed (1973: 230) for *A. ameiva* from Surinam, except that the last (fourth) supraocular is much smaller than the first (subequal fide Hoogmoed). One specimen has an azygous scale between the interparietal and the right parietal at their posterior borders.

Ameiva ameiva tends to be a large lizard: Echternacht (1971) reported maximum snout-vent lengths of 157 mm (♀) and 197 mm (♂) in Panama; Hoogmoed (1973) gave maxima of 131 mm (♀) and 168 mm (♂) for Surinam. Total length may exceed half a meter; Beebe (1945: 9) gave maximum total lengths of 465 mm (♀) and 535 mm (♂). Ameivas this large make themselves conspicuous as they forage about or plunge through dry vegetation when alarmed. We neither saw nor heard lizards of such size. The largest specimens are males of 98 mm and 112 mm SVL; these have swollen testes 4–5 mm long. The largest female is only 91 mm SVL but is sexually mature as shown by the presence of two small (1.5–2.1 mm) eggs high in each oviduct.

All specimens have broad, dark brown lateral stripes extending over the ear from behind the eye to the groin. This broad stripe is bordered by light stripes dorsally and ventrally, but the dorsal light marking is only conspicuous to the posterior margin of the arm. All except the two smallest (50, 54 mm SVL) have dark spots on the throat.

Neusticurus racenisi Roze
Figures 22–23

Neusticurus racenisi Roze, 1958a: 252–257, figs. 5–8. Holotype AMNH 61008 from base Auyantepui, 400 m, Estado Bolívar, Venezuela, collected by W. H. Phelps.

MATERIAL: AMNH 136195–136197, Summit Camp 1.

We found three specimens of *Neusticurus racenisi* along the small forest stream where they were sleeping at night, on vegetation approximately 1 m above water's edge. A juvenile (63 mm SVL) was lying horizontally on a fern frond; an adult female and male (86 mm and 105 mm SVL, respectively) were clinging to herbaceous vegetation with their heads pointed towards the water. They awaken and become wary when approached at night; a few animals probably of this species were heard dropping into the stream ahead of us.

REDESCRIPTION

We compared the Guaiquinima specimens of the little-known *Neusticurus racenisi* with the holotype (AMNH 61008) and paratype (AMNH 61040) from nearby Auyantepui (Roze, 1958a) and also utilized the data provided by Van Devender (1969) for material collected at Cerro Duida. The following description expands on Roze's (1958a) original one and includes variation observed in the western (Cerro Guaiquinima) and southern (Cerro Duida) samples.

SQUAMATION: Rostral plate wider than high and in contact laterally with the nasal and first supralabial, dorsally with the frontonasal. Frontonasal single, in contact laterally with nasal and anterior corner of loreal. The holotype has a small triangular scale at the left posterior margin of the frontonasal; the paratype has a small triangular scale and two granules between the frontonasal and the scales posterior to it; Duida specimens have one or two frontonasals. There are 18–32 small, irregularly shaped scales posterior to the frontonasal and anterior to the parietals (18 in holotype); 3–5 scales posterior to the frontonasal; two rows of scales between supraoculars, with 4–6 scales in each row; three specimens (AMNH 61008, 136196, 136197) have 1–4 small, median azygous scales between the rows. Interparietal usually longer than parietals (except in AMNH 136196). The interparietal is slightly longer than wide and wider than the right parietal in the paratype. The parietals are longitudinally divided into four plates in AMNH 136196. There are 16–18 small flat plates behind the parietal series (16 in Guaiquinima sample, 18 in Auyantepui types), decreasing in size laterally. The occipital and temporal regions are covered by juxtaposed granular or conical scales. Supraoculars 4/4 or (in AMNH 136197) 5/4. Superciliaries 7–10 (holotype, 9/8); 6–10 granules between superciliaries and supraoculars (holotype 9/9). The transparent disc in the lower eyelid comprises 5–6 palpebrals in the Guaiquinima lizards (4/4 in holotype,

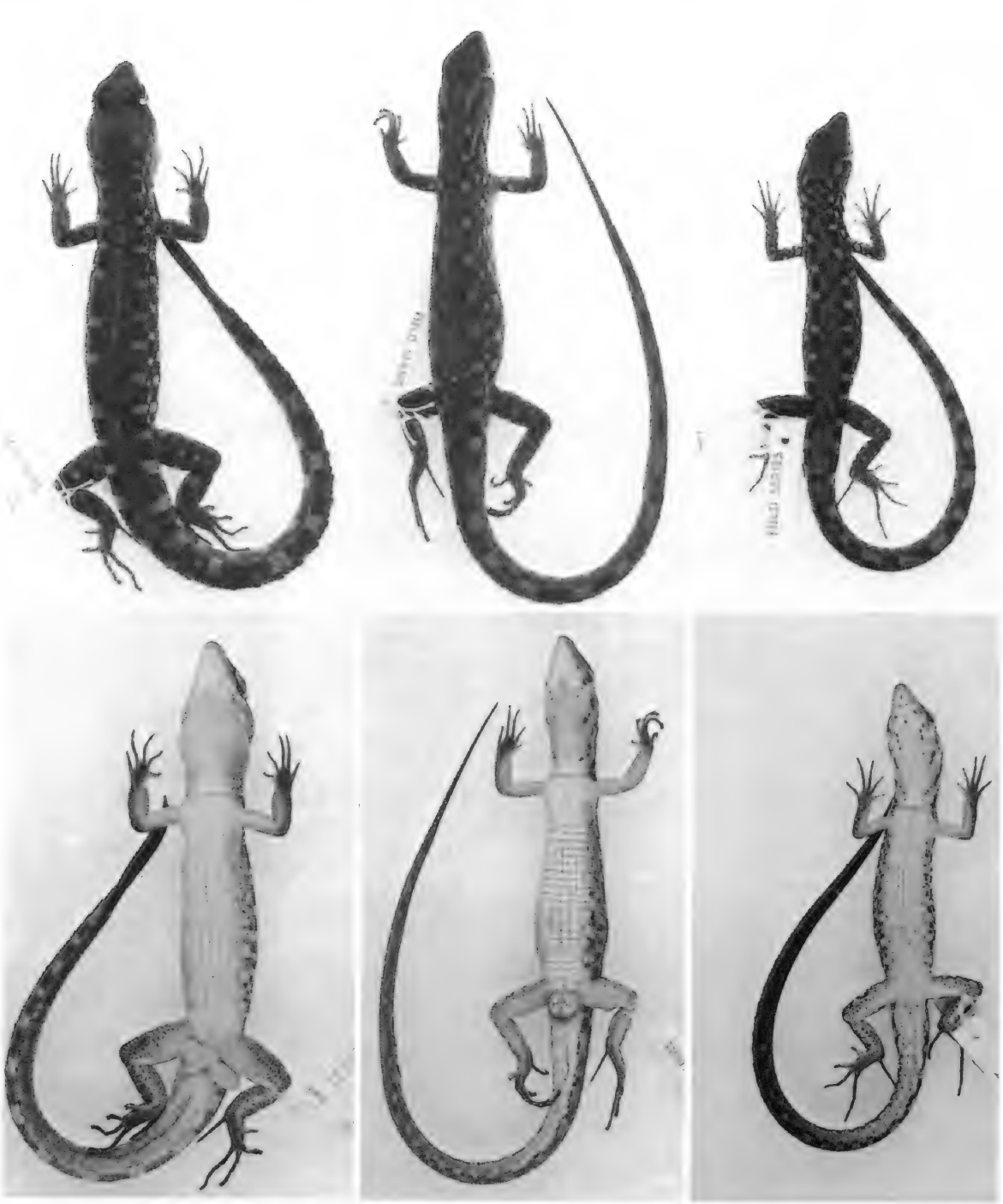

Fig. 22. *Neusticurus racenisi* from Cerro Guaiquinima. From left to right: AMNH 136195, adult ♂ ×0.62; AMNH 136196, adult ♀ ×0.65; AMNH 136197, juvenile ×0.75.

4/5 in paratype). The loreal is divided on the right side in AMNH 136196 and on both sides in the paratype. Postoculars 7–9 (8/7 in holotype); dorsal postocular largest. Well-developed external auditory meatus, tympanum recessed.

Supralabials 7–9 (holotype, 8/8); the fourth supralabial under center of eye, posterior two

smallest. Infralabials 4/4 or (in AMNH 136197) 3/3. Two enlarged pairs of chin shields and 1—2 pairs of smaller shields behind these. Anterior gulars smooth, elongate, juxtaposed; posterior gulars rounded. Throat medially with small, round juxtaposed scales, becoming conical laterally. Anterior to margin of gular collar, 5–6 rows of enlarged imbricate, smooth, round to rectangular scales in the middle of throat (holotype, 5 rows). Small round, juxtaposed granules under the collar.

Nape covered with juxtaposed conical scales. increasing in size and becoming more rounded laterally. Middorsal scales large, keeled, juxtaposed. Dorsolateral scales from arm onto tail enlarged, keeled, in five rows. Lateral scales decreasing in size and more granular.

Anterior 9–12 rings of caudal scales dorsolaterally containing large keeled scales, followed posteriorly by two distinct paravertebral crests separated medially by 2–3 small, flat juxtaposed scales. Laterally viewed, tail vertically arranged in single rings of large keeled scales separated by 3–4 rings of smaller keeled scales. Ventrals in 29–32 transverse rows (30 in holotype). One female with 8/7 preanal-femoral pores, males with 33–38 (holotype, 35/37).

Dorsal and posterior surfaces of arm, and anterior surface of upper arm, with large, ridged, slightly imbricate scales having a central keel decreasing in size posteriorly. Large flat imbricate scales on anterior surface of the lower arm. Ventral surface of forelimb with round or conical scales. Dorsal surface of hand and proximal scales of fingers with ridged, imbricate scales. Subdigital lamellae of fingers smooth and usually entire (occasionally divided).

Anterior surface of thigh with large, keeled imbricate scales; dorsal and posterior surfaces of leg, and anterior surface of lower leg, with smaller, keeled, slightly imbricate scales. Ventral surface of leg with large, smooth imbricate scales. Scales on dorsal surface of foot and all but the terminal scale on toes are ridged, keeled, and imbricate; terminal scale on toe smooth. Subdigital lamellae of toes proximally divided and distally entire. Palms and soles with small round, smooth, juxtaposed scales.

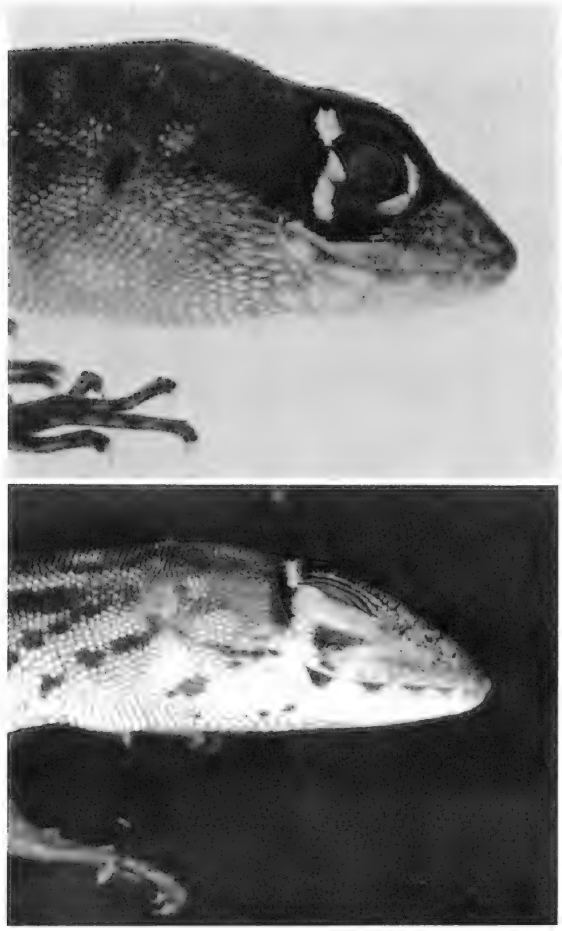

Fig. 23. *Neusticurus racenisi* from Cerro Guaiquinima, showing sexual dimorphism in color pattern. Adult ♂ (AMNH 136195) top, adult ♀ (AMNH 136196) bottom; both ×2.

Coloration In Life (Cerro Guaiquinima): Head blackish brown above; nape and middorsum dark dull brown (♂) or brown (♀ and juv.); a dorsolateral line of olive-brown (♂) or pale brown (♀ and juv.) squarish spots. Ground color of dorsolateral area and side of body dark red-brown (♂) or black (♀ and juv.) turning brighter and lighter ventrally; pale yellow (♂) or tan lateral spots and speckling. Side of tail checkered with dark brown and light orange (♂) or paler brown.

Pale preocular and postocular markings vivid pale blue (nearly white) in male, golden yellow and less well defined in female and juvenile. Loreal region and upper lip light orangish brown in male (not noted but probably duller brownish in ♀ and juv.). Iris dark

brown (♂) or pale orange anteriorly and gray posteriorly (♀). Anterior half of tongue blackish gray above, unpigmented basally and ventrally (notes for ♂ only).

Chin, venter, and undersides of hind limbs bluish white, with throat and undersides of forelimbs suffused pale brown (♂); or ventral surfaces pale tan, with a greenish sheen on venter (♀ and venter).

NOTES ON COLOR PATTERN (Guaiquinima and Auyantepui): Dorsum brown with 11–12 dorsolateral, squarish tan spots, which continue onto tail (regenerated portions lack spots); also square spots ventrolaterally on tail. Sides of body below dorsolateral square spots with 2–3 rows of light spots from arm to hind limb; in males (AMNH 136195 and holotype), the anteriormost of these spots have darker centers and are outlined in black. Limbs distinctly pale spotted above.

Orbital region black in males (AMNH 136195 and holotype), with distinct preocular and postocular white markings; the preocular mark curves around the anterior part of the eye, the postocular mark is vertically aligned, extending from the superciliaries to the posterior subocular. In females (AMNH 136196) and juveniles (AMNH 61040 [paratype], 136197), the orbital region is less dark and the postocular mark is distinct but the preocular mark is not. The female and juveniles with three dark stripes extending from tympanum to level of arm, the upper stripe horizontal and the lower two slanted posteroventrally in parallel; postympanic stripes separated by pale areas.

REMARKS: Uzzell (1966) synonymized *Neusticurus racenisi* under the name *N. tatei*, from which it was resurrected by Van Devender (1969), who implied near sympatry for these species. Dixon and Lamar (1981) suggested that *Neusticurus medemi* from Colombia is the closest relative of *N. racenisi*. The last two species are certainly similar ecologically, both perching over water along small forested creeks.

Neusticurus species, cf. *Neusticurus rudis* Boulenger

Figure 24

Neusticurus rudis Boulenger, 1900: 53–54, pl. 5, fig. 1. Holotype BMNH 1946.8.31.64 from base of Mount Roraima, about 3500 ft, Guyana, collected by F. V. McConnell and J. J. Quelch.

MATERIAL: AMNH 136204–136208, Summit Camp 1; AMNH 136198—136203, Summit Camp 2.

NATURAL HISTORY: *Neusticurus "rudis"* was active during the day and always found in water or on rocks next to water, being most common in a quiet headwater pool in heavy vegetation (fig. 7A) but also occurring along open rocky stream banks (e.g., fig. 4). They swim in a serpentine fashion with the head held above water. When disturbed, they would dive into the water, or submerge if swimming, and swim underwater to the edge of the pool to hide under overhanging vegetation or rock ledges. At Camp 2, one individual escaped by running from a pool into dense vegetation surrounding the pool. Four of the 11 specimens had broken or regenerated tails when captured.

COLOR PATTERN: Brown in life, with paler dorsolateral markings and variable black spotting atop body and tail, flanks blackish. Dark flank color extends anteriorly to neck in three individuals, but side of neck paler and with a distinct black spot in most specimens. One or two rows of light spots (yellowish in at least one living specimen) on sides of body and tail, the caudal spots most distinct near tail base. Anterior and posterior limb surfaces, and frequently dorsal surfaces of forelimbs, light spotted. Sides of face usually light spotted.

Labials and throat whitish with or without gray markings; throat distinctly striped in smallest individuals and some adults with indistinct gular markings. Rest of ventral surfaces pale greenish white (yellowish white in preservative), becoming dark brown posteriorly under tail; lateral ventral scales with aggregations of minute black dots; palms, soles, and undersides of digits dark gray. Iris either gray or black with a bronzy rim around pupil.

REMARKS: Squamation in the Guaiquinima sample differs from the descriptions provided by Boulenger (1900) for the holotype of *Neusticurus rudis*, by Uzzell (1966) for the species, and by Hoogmoed (1973) for Surinam specimens. This name represents either a highly variable lizard or it includes more

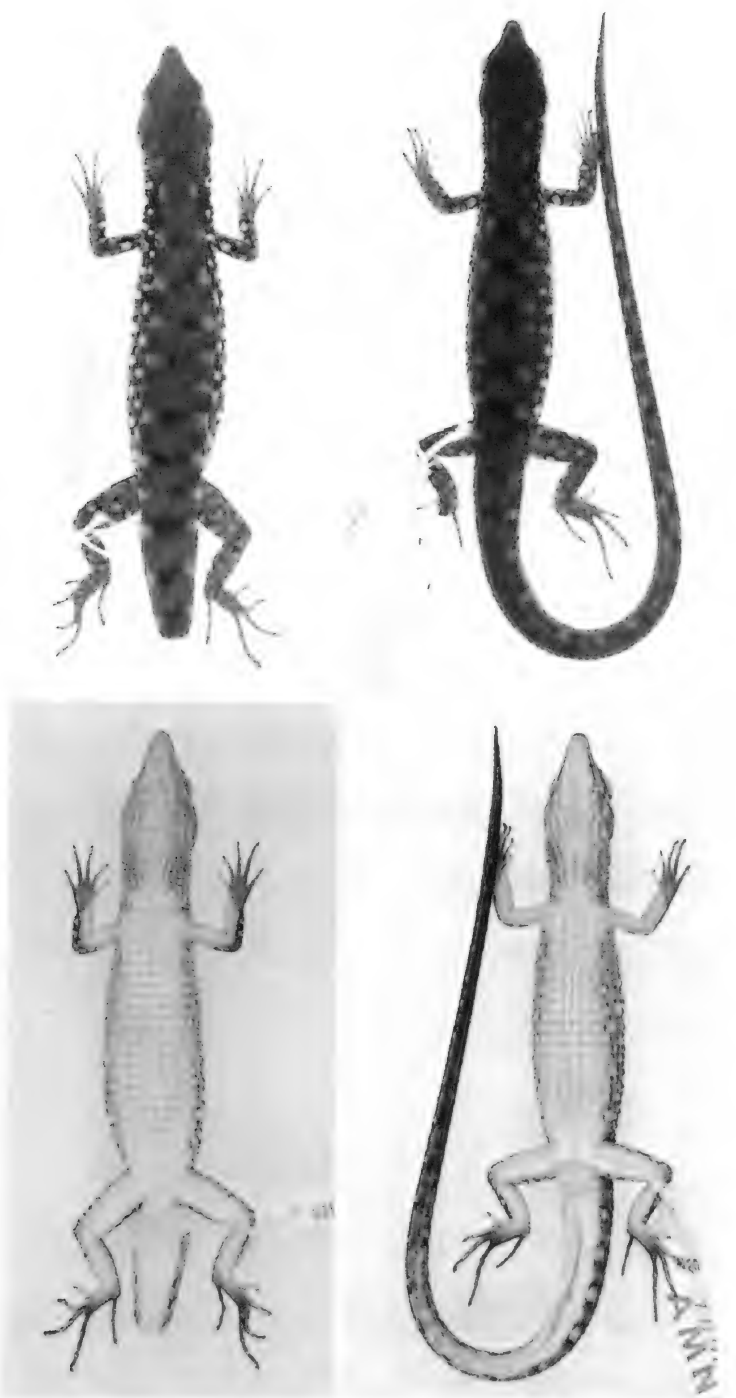

Fig. 24. *Neusticurus* sp., cf. *N. rudis* from Cerro Guaiquinima. **Left,** adult ♂ ×0.85 (AMNH 136199). **Right,** adult ♀ ×1.06 (AMNH 136205).

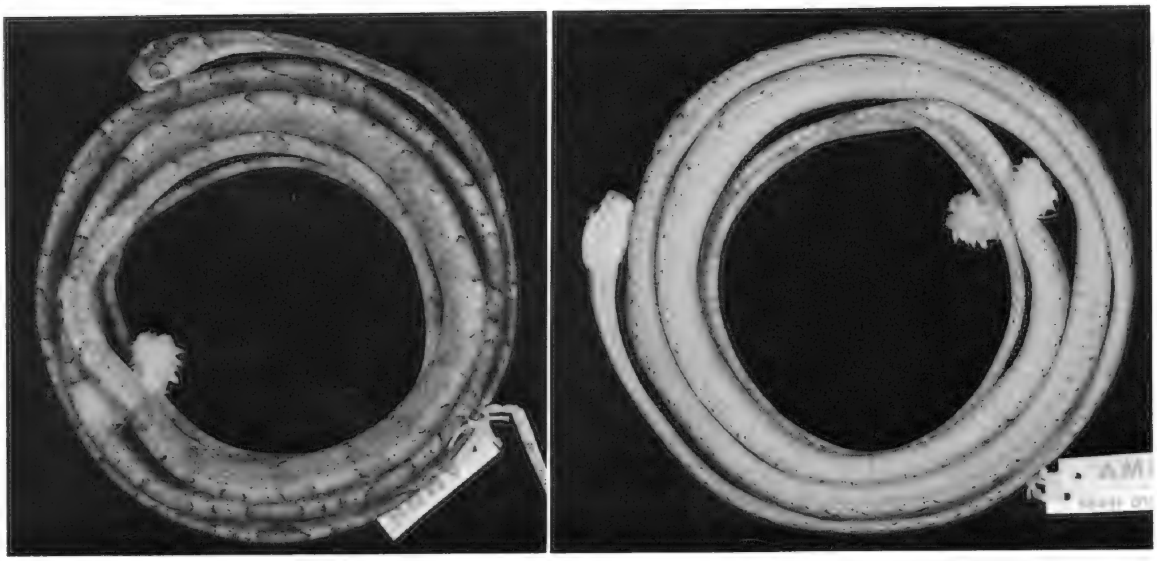

Fig. 25. *Imantodes lentiferus* (AMNH 136209) from Cerro Guaiquinima, representing the first record of this blunt-headed vine snake from Venezuela, ×0.68.

than one species, a problem which the first author is currently pursuing.

SNAKES

FAMILY COLUBRIDAE

Imantodes lentiferus (Cope)

Figure 25

Himantodes lentiferus Cope, 1894: 613–614. Lectotype ANSP 11459, designated by Myers (1982: 35), from upper Amazon drainage, either Pebas, Peru, or eastern Ecuador, obtained either by J. Hauxwell or J. Orton.

MATERIAL: AMNH 136209, Summit Camp 1.

A very large male was loosely coiled atop a palm frond about 1.5 m aboveground, at night in the tall forest south of camp. It is 1036 mm total length, 316 mm tail length (tail/total = 0.310); 15–15–15 dorsal scale rows, with scales in vertebral row large, with concave to truncate rear margins, ≥ 2 times wider than midlateral scales; 228 ventrals; undivided anal plate; 130 subcaudals; 1/1 preoculars; 2/2 postoculars; 8/8 supralabials; 10/10 infralabials; 1 + 2 temporals.

In life, a dark-speckled, light-brown ground color with partially black-edged, medium-brown dorsal blotches (44 on body, 25 on tail). Head pattern including three brown spots forming a Y-shaped marking. Supralabials pale yellow; underside of head white, rest of ventral surfaces pale greenish brown with dark speckling. Iris light yellowish brown. Tongue light gray except tips of fork unpigmented.

REMARKS: The snake agrees with the description for this species given by Myers (1982), although the total length exceeds the previous maximum (1015 mm) for males. The everted hemipenis is similar to those illustrated in Myers (op. cit., fig, 18) except that the spines, including those in the asulcate "oblique cluster," are relatively larger. The oblique cluster interrupts the overhang of the hemipenial capitulum on its asulcate side and is evidence of sister-species relationship with *Imantodes phantasma* of eastern Panama.

Imantodes lentiferus has not been recorded previously from Venezuela (Roze, 1966; Peters and Orejas-Miranda, 1970; Myers, 1982). Myers (1982: 39) noted that this vine snake shows a fairly uniform phenotype throughout its vast range in the Amazonian drainage, but that specimens from Surinam and French Guiana look quite different owing simply to absence of dark edging around the dorsal blotches. The Guaiquinima specimen, with partially dark-edged blotches, is somewhat intermediate between these two pattern

Fig. 26. *Liophis torrenicola*, n. sp.. Adult ♂ holotype (AMNH 136211), ×1.09.

types—dorsally it seems closest to the Amazonian condition, but laterally the blotches are even less pronounced than in snakes from eastern Guayana (compare fig. 25 this paper with figs. 16B–17 in Myers, op. cit.).

Liophis torrenicola, new species
Figures 26–28A, 29

HOLOTYPE: AMNH 136211 (field no. CWM 18983), an adult male caught by C. W. Myers

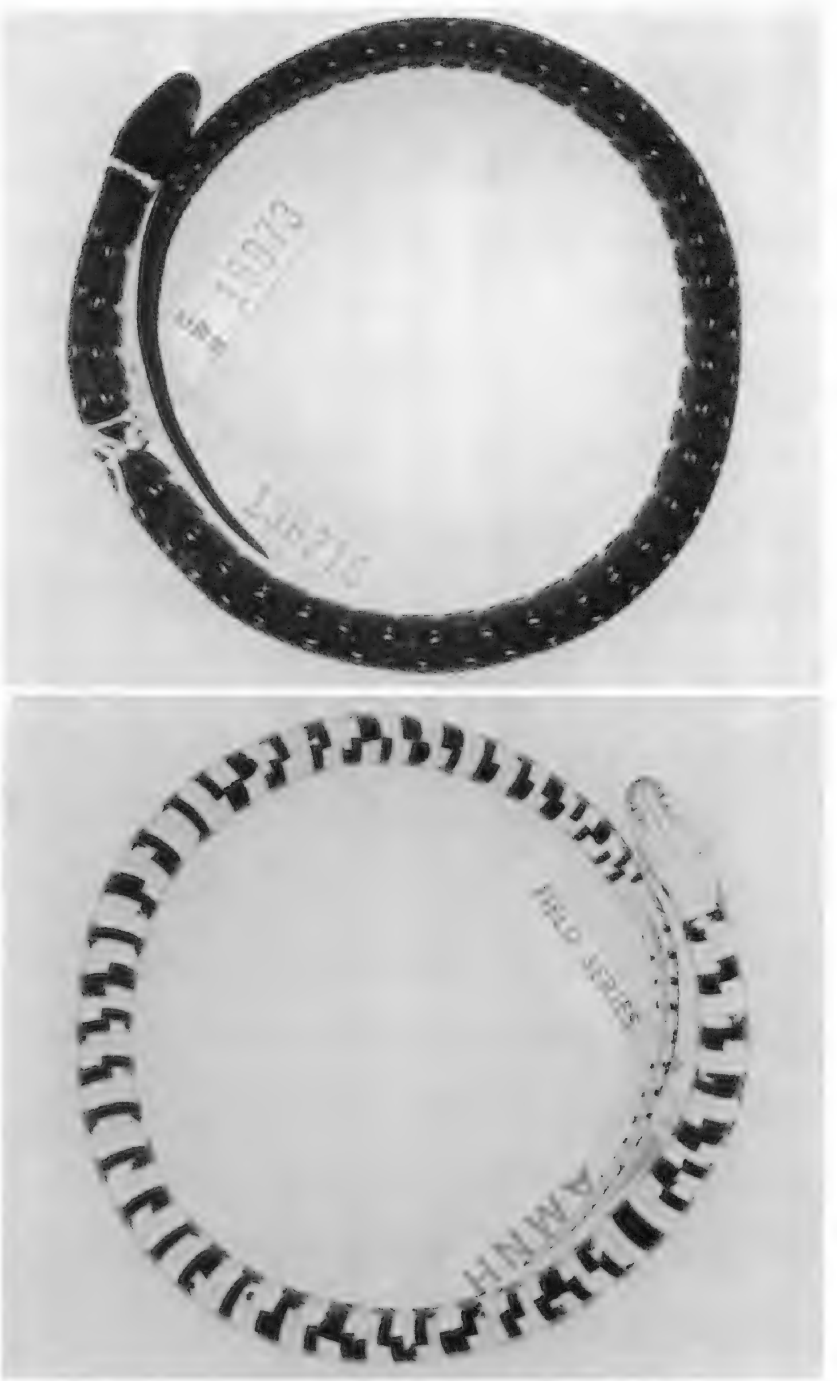

Fig. 27. *Liophis torrenicola*, n. sp. Juvenile paratopotype (AMNH 136210), ×1.23.

and M. A. Donnelly on February 26, 1990, at Summit Camp 1, 1030 m elevation, north side of Cerro Guaiquinima, Bolívar, Venezuela.

PARATOPOTYPE: AMNH 136210 (field no. CWM 18973), a juvenile male caught on February 24, 1990; other data as for holotype.

ETYMOLOGY: The species name, a noun in

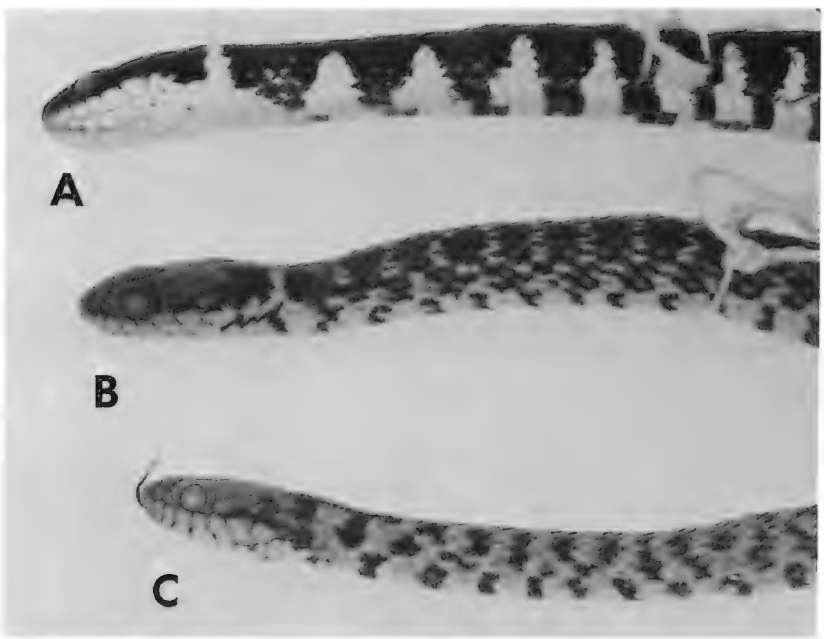

Fig. 28. Anterior color patterns of juvenile *Liophis*, ×2. **A.** *L. torrenicola*, new species (AMNH 136210, paratopotype). **B.** *L. cobella* (AMNH 36135, Georgetown, Guyana). **C.** *L. cobella* (AMNH 18158, Kartabo, Guyana).

apposition, is derived from the Latin *torrens* (a swift or violent stream) + connective *-i* + the suffix *-cola* (inhabitant).

DIAGNOSIS: A *Liophis* of the *cobella* group (sensu Dixon, 1983: 149), distinguished from the geographically proximate *L. c. cobella* as follows: (1) by greater number of ventrals (168, 173 in ♂ *torrenicola*, vs. 143–164, $\bar{x}$ = 151.6 in *cobella*);[11] (2) by white to orange ventral surfaces in life (red in *cobella* fide Beebe, 1946, Dixon, 1983); (3) by a distinct pale neck ring (figs. 26–27, 28A) persisting into maturity (less well defined ring present or absent in juvenile *cobella* [fig. 28B, C] but lost in adults); (4) by a juvenile pattern (faint in adult) on the side of the body showing alternating dark and light triangular bands (vague banding not triangular in young *cobella*, cf. fig. 28A–C).

The laterally triangular juvenile blotches and the neck ring also may distinguish *Liophis torrenicola* from the two other named Venezuelan tepui species. Also, *L. torrenicola* has a dark-checkered venter with a considerable extent of pale ground color (figs. 26, 27), whereas *L. trebbaui* (Auyantepui) differs in having the ventral black markings forming broad transverse bands about the width of two ventral plates (fide Roze, 1958a, fig. 11 and text description of the types). *Liophis ingeri* (Chimantá Tepui) agrees with *L. trebbaui* and not with *L. torrenicola* in having an extensively black-marked venter that is as much cross-banded as checkered (fig. 31), but *L. ingeri* differs from both *L. torrenicola* and *L. trebbaui* in having posterior head plates and anterior body scales vaguely pale spotted or reticulated (fig. 30, and Roze, 1958b).

DESCRIPTION

The holotype (fig. 26) is an adult male as judged by hardened hemipenial spines. The paratopotype (fig. 27) is a juvenile male.

[11] Unfortunately, Dixon (1983) did not separate his data for male and female snakes. Taking the usual sexual dimorphism into account, one assumes that the higher ventral counts in the range given for *L. c. cobella* are for females—thus further increasing the distance from the male types of *L. torrenicola*. Two other "subspecies" of *cobella* (*dyticus* and *taeniogaster*) have still lower numbers of ventrals (means for combined sexes = 138 and 149, respectively, fide Dixon). We recognize *L. cobella trebbaui* sensu Dixon (ventrals > 170) as comprising two distinct tepui species, *L. trebbaui* and *L. ingeri*.

PROPORTIONS AND SCUTELLATION: Adult male a small, moderately robust snake 457 mm total length, tail 79 mm (17.3% of total length); juvenile male 245 mm total, 42 mm tail length (17.1%). Body about as wide as high, slightly angular ventrolaterally. Head slightly distinct from neck, narrower than body in adult, wider than body in juvenile; greatest head width across temporal region 60 percent (juv.) or 65 percent of head length (tip of snout to end of mandible). Diameter of eye slightly more (juv.) or less distance from its anterior edge to edge of naris, extending 1.4 (juv.) or 1.7 times into length of snout. Dorsal scales smooth, lacking apical pits and anal ridges, in 17-17-15 rows; scale-row reduction to 15 rows occurring past midbody by fusion of rows 3 + 4 at level of ventrals 116/115 (juv.) or 118/114. Two preventrals (undivided gulars) in adult male holotype + 175 ventrals + 56 subcaudals; one preventral in juvenile male + 168½ ventrals (ultimate plate a "half-ventral") + 54 pairs of subcaudals. Anal plate divided.

Rostral plate visible from above, wider than high. Paired internasals about as wide as long, somewhat rounded at corners and narrowed in front, two-thirds the length of prefrontals. Paired prefrontals wider than long, each in contact with its mate and with frontal, supraocular, preocular, loreal, nasal, and internasal. Frontal slightly pentagonal (nearly triangular in holotype), 1.5–1.6 times longer than its greatest (anterior) width, 1.1–1.4 times longer than distance from its anterior edge to tip of snout. Supraoculars large, 81 (juv.) or 97 percent of frontal length, anteriorly narrowed, posteriorly wider than adjacent part of frontal. Parietals 1.4–1.6 times longer than broad; interparietal suture 84–89 percent of frontal plate, slightly longer (juv.) or slightly shorter than snout length.

Nasal plate in contact with supralabials 1–2, deeply grooved or divided above and below naris. Loreal plate irregularly shaped, higher than long. Single large preocular. Two postoculars, the lower smaller than upper, except these scales fused into one high plate on left side of paratopotype. Temporals 1 + 2, the upper secondary temporal much larger than lower and also larger than primary temporal. Supralabials 8/8, with 2–3 touching loreal and 4–5 bordering orbit. Infralabials 10/9 (juv.) or 10/10, first pair in contact behind mental, 1–5 touching an anterior genial, 5–6 touching a posterior genial. Genials well developed, anterior pair little larger than posterior pair; posterior genials completely separated by azygous scales in holotype but touching in paratopotype. Minute head-plate tubercles (presumed sensory organs) most concentrated on snout.

COLORATION: In life, the juvenile male paratopotype had a black head set off by a bright yellow neck ring. Middorsum was dark brown, with small yellow paravertebral spots set in vague black mottling. Sides of the body with alternating black and yellow triangular bars on the sides—the yellow bars with apices pointing dorsad in line with the yellow dorsolateral spots. Supralabials pale yellow; chin white with dark smudging; ventral and subcaudal surfaces yellowish white, with black checkering on the belly represented by lateral black markings under the tail.

The pattern was less vivid in the adult male holotype, whose head and dorsum were dark brown in life, lacking yellow paravertebral spots and with a less sharply defined grayish green neck ring and parietal spots (parietal markings absent in juvenile). Sides of the body with ventrad extensions of the dorsal brown color (corresponding to the lateral black markings in the juvenile), separated by vaguely triangular grayish green interspaces. Supralabials and underside of head (chin dark smudged) and neck yellow, turning bright orange over the rest of the black-checkered ventral and subcaudal surfaces. The iris in both was dark red-brown and the tongue was black.

In preservative, after some fading, an ill-defined black postocular stripe is discernible in both specimens, extending from the postoculars and across the tops of the last few supralabials toward the neck ring.

MAXILLARY DENTITION: As examined in situ and counting empty sockets, the paratype has 17 + 2 (left) and 18 + 2 (right) maxillary teeth, and the holotype has 19 + 2 on each side. The ultimate prediastemal socket lies posterior to the anterior edge of the ectopterygoid process.

HEMIPENIS: The everted hemipenis (fig. 29) extends to the end of subcaudal 6. The organ is bilobed with well-defined nude apical discs. The sulcus spermaticus divides midway up

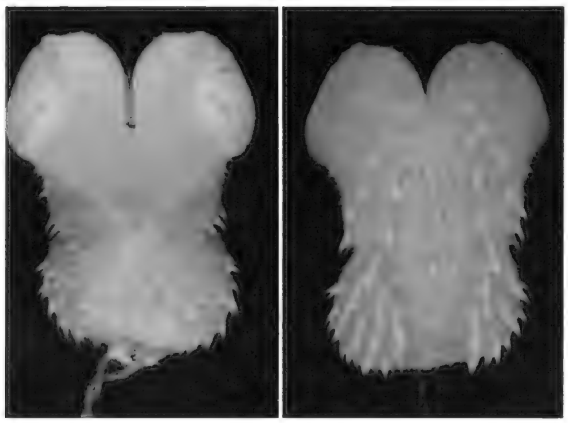

Fig. 29. Hemipenis of *Liophis torrenicola*, new species. Left everted organ of holotype (AMNH 136211), ×3. **Left,** sulcate side; **Right,** asulcate side.

the organ and its branches diverge centrifugally, each reaching the apex through a deep lateral cleft in the apical disc. The organ is spinose, the spines small on the short lobes around the apical discs and small to medium size proximally, with an intermixing of spinules; the crotch is nude.

Habitat and Natural History

Both of our specimens of *L. torrenicola* were collected during sunny afternoons along the north stream in scrubby *Stegolepis-Clusia* savanna (fig. 4). The juvenile was lying in a shallow pool with a rock bottom. The holotype was in deeper water at the side of a rocky pool, with a small fish (*Piabucina uruyensis* [det. C. J. Ferraris, Jr.]) in its mouth. A third individual that was seen by other members of our party escaped by diving and hiding among rocks.

Remarks

Dixon (1983) combined two species of tepui snakes (*L. trebbaui* Roze, 1958a, and *L. ingeri* Roze 1958b) into a single geographic race of the lowland *Liophis cobella*. Dixon (1983: 159) expected that increased knowledge of variation in the number of ventrals of tepui snakes would come to minimize the known differences between *L. c. cobella* (143–164) and *L. c. trebbaui* (171–179, $N = 4$). The two specimens of *Liophis* from Cerro Guaiquinima also have high ventral counts (168,

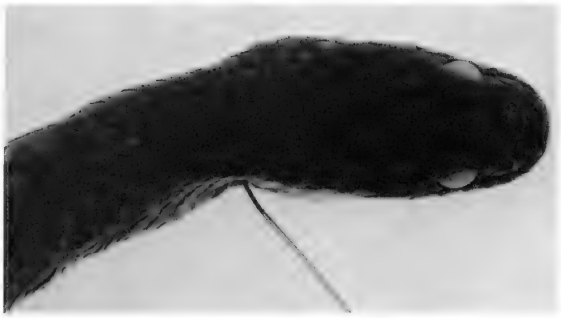

Fig. 30. Head and neck of *Liophis ingeri* (FMNH 74038, ♂ holotype from Chimantá Tepui), ×2. Possibly diagnostic pale spotting on the head plates and anterior body scales are still weakly discernible on this 37-year-old specimen.

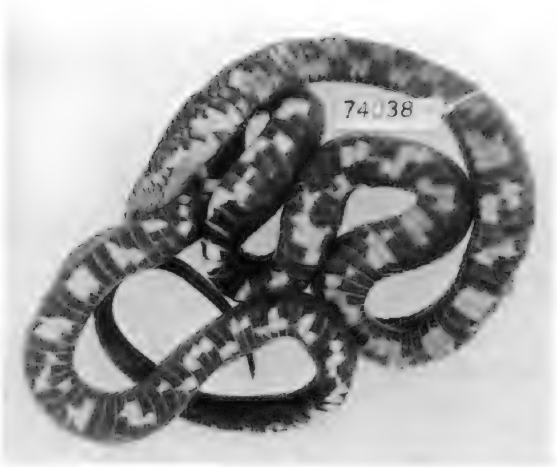

Fig. 31. *Liophis ingeri* (FMNH 74038, ♂ holotype from Chimantá Tepui), in ventral view, ×0.6.

173) and the difference between high and low counts for the six specimens known from Venezuelan tepuis is only 11 (sexes combined, see note on page 43), much less than that for the other subspecies (18–22) recognized by Dixon. Segmental counts in snakes are sometimes sensitive indicators of geographic change (e.g., latitudinal, mainland vs. insular) and it is at least conceivable that high ventral counts of tepui *Liophis* might be partly the result of some environmental factor correlated with elevation. Nonetheless, this is not known and we tentatively accept the ventral counts as a taxonomic character equal to others.

The three known tepui populations appear

to be well isolated from one another and from their geographically closest lowland relative (*L. c. cobella*), and their ventral counts are significantly higher than those of other populations assigned to *L. cobella* sensu Dixon. For these reasons, and because each of the three tepui populations seem also to have differentiated in coloration to some degree, we describe *Liophis torrenicola* as new and resurrect *Liophis ingeri* from the synonymy of *L. c. trebbaui*, with the latter being again elevated to specific status in its original sense.

According to Dixon (1983), triangular lateral light bands occur in the *cobella* group only in *L. frenatus* and *L. longiventris*—Brazilian species found well south of the Amazon. These markings also characterize the new *Liophis torrenicola* and are, in our view, a strong indication that the tepui isolates are something other than relictual populations of the lowland *L. cobella*.

Philodryas cordata, new species
Figures 32, 33

HOLOTYPE: AMNH 136212 (field no. CWM 18974), an adult male caught by C. W. Myers on February 24, 1990, at Summit Camp 1, 1030 m elevation, north side of Cerro Guaiquinima, Bolívar, Venezuela.

ETYMOLOGY: The species name is derived from the Latin *cordis* (genitive of *cor*, the heart) + *-atus*—meaning, in the present connection, "heart-shaped," in allusion to the everted hemipenis (see fig. 33). It is an adjective given in feminine form as demanded by the generic name, which is of feminine gender.[12]

[12] This assertion requires explanation inasmuch as *Philodryas* historically has been treated as masculine (e.g., by Boulenger, 1896; Peters and Orejas-Miranda, 1970; Thomas, MS). The gender of *Philodryas* is determined by its ending, and, indeed, there is a masculine *Dryas* (with meanings of: the father of Lycurgus, king of Thrace; or one of the Lapithæ; or a party of the Calydonian hunt). But the generic name actually is based on the other *Dryas*, a spirit who is physically and grammatically feminine. In a footnote to the original description of *Philodryas* (type species *Coluber Olfersii* Lichtenstein), Wagler (1830: 185) derived the name as follows: "Φιλος amicus, et δρυας Sylvae Nympha (ovid.)." Thus, *Philos* (friend or friendly) + *dryas* (tree nymph) seems to convey the notion of friendly tree snakes—quite inappropriate for somewhat poisonous snakes that bite vigorously!

DIAGNOSIS: A tan *Philodryas* readily distinguished from all other species occurring north of the Amazon in being tan in life rather than green. The species furthermore seems to differ from all other *Philodryas* in color pattern and penial characters (see Remarks).

DESCRIPTION OF HOLOTYPE

The specimen (fig. 32) is an adult male as judged by the hardened hemipenial spines.

PROPORTIONS AND SCUTELLATION: A small racerlike snake 740+ mm total length, 223+ mm tail length (small section of end of tail lacking); tail length about 30 percent of total length. Body slightly wider than high, rounded ventrolaterally. Head distinct from neck, slightly narrower than greatest body width; greatest head width (temporal region) 11.6 mm, head length 21.9 mm from tip of snout to level of end of mandibles. Diameter of eye (3.8 mm) greater than distance from its anterior edge to edge of naris (3.3 mm), extending 1.6 times into length of snout (6.0 mm). Dorsal scales smooth, with single median apical pits anteriorly, lacking anal ridges or tubercles, in 19-19-15 rows; scale-row reduction occurring slightly past midbody, from 19 to 17 rows by fusion of rows 8 + 9 at level of ventrals 106/107 and then to 15 rows by fusion of rows 3 + 4 at ventrals 108/107. Two preventrals (undivided gulars), 172 ventrals, divided anal plate, 107+ pairs of subcaudals (lacking only the terminal few).

Rostral plate well visible from above, 1.6 times wider than high. Paired internasals nearly as long as wide, 75 percent as long as prefrontals. Paired prefrontals wider than long, each in contact with its mate and with frontal, supraocular, preocular, loreal, nasal, and internasal (left prefrontal in contact with both left and right internasal). Frontal pentagonal, 1.7 times longer than its greatest (anterior) width, 1.1 times longer than distance from its anterior edge to tip of snout. Supraoculars large, 90 percent of frontal length, anteriorly slightly narrowed, posteriorly wider than adjacent part of frontal. Parietals 1.5 times longer than broad; interparietal suture 84 percent length of frontal plate, roughly equal to snout length.

Nasal plate in contact with supralabials 1–2, divided above and below naris. Loreal plate

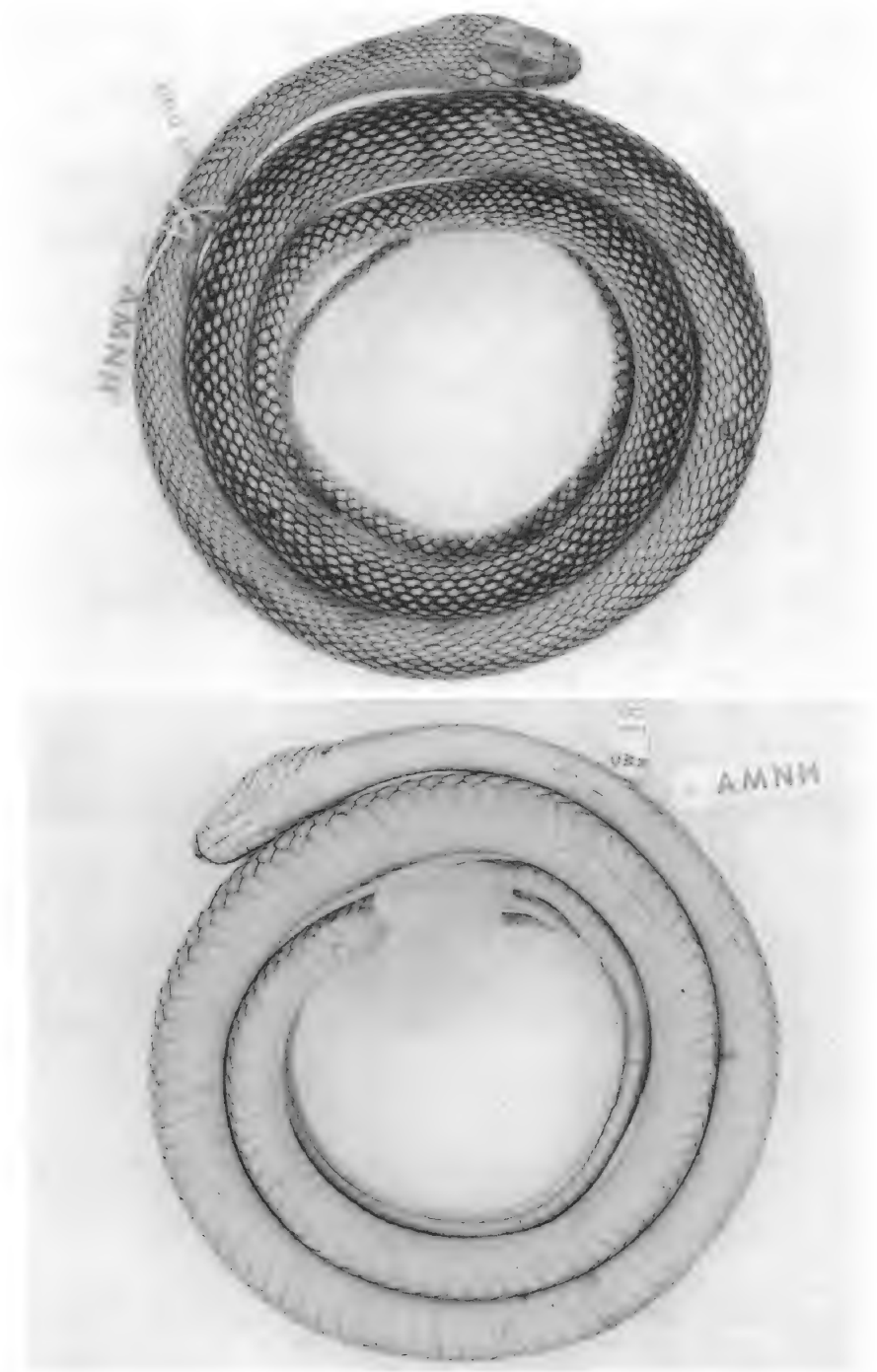

Fig. 32. *Philodryas cordata*, n. sp. Adult ♂ holotype (AMNH 136212), ×0.84.

rhomboidal. Single large preocular; three small postoculars, variable in size but uppermost one largest on each side. One large anterior temporal and smaller upper and lower posterior temporals (upper secondary tiny on left side, larger than lower secondary on right side), for a formula of 1 + 2. Supralabials 8, with 2–3 touching loreal and 4–5 bor-

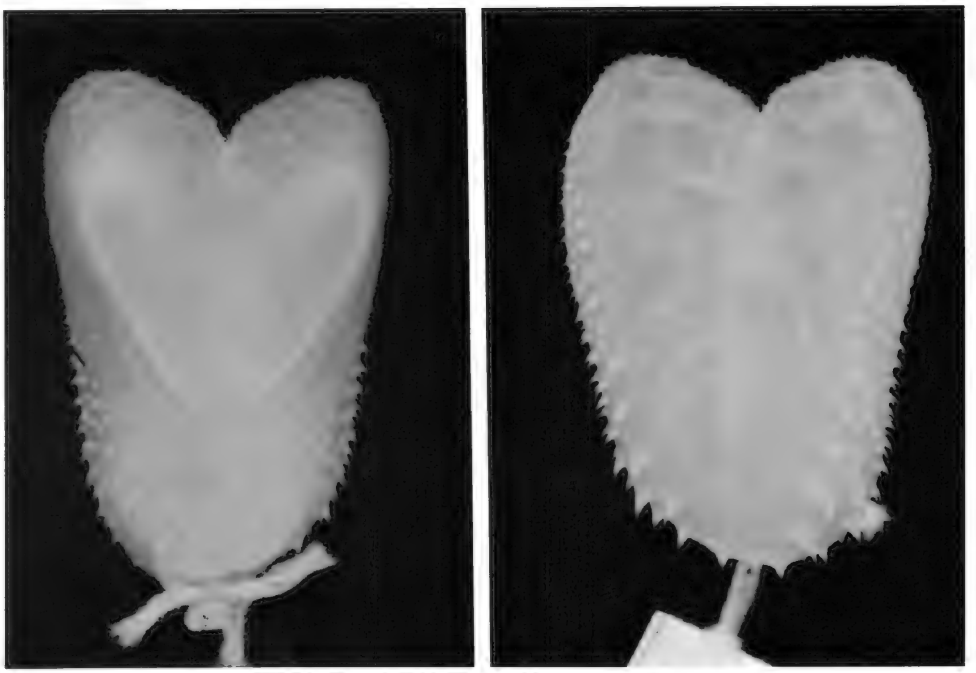

Fig. 33. Hemipenis of *Philodryas cordata*, n. sp. Left everted organ of holotype (AMNH 136212), ×3. **Left,** sulcate side; **Right,** asulcate side.

dering orbit. Infralabials 11 (ultimate one on left side very small), first pair in contact behind mental, 1–5 touching an anterior genial, 5–6 touching a posterior genial. Genials well developed, anterior pair larger (longer and wider) and with a much longer suture than posterior pair. Inconspicuous tubercles (presumed sensory organs) sparsely scattered over all dorsal and ventral head plates.

COLORATION: A handsome snake in life—overall tan, with contrasting black scale edges; gray skin between scales (seen when scales were spread by hand). Supralabials also tan. All ventral surfaces overall silvery white. Iris black with a few silver flecks at top. Tongue, including fork, black.

The black scale-edging is heaviest on scales in the vertebral region anteriorly, this area widening posteriorly so that scales in the median seven scales rows are mostly black with pale centers. The intensification of black on the edges of scales on the middorsum does not, however, give the impression of a dorsal dark stripe.

In preservative, the tan color turned a slightly darker brown and then, after loss of the stratum corneum, again pale tan (most of snake) or very pale blue (especially posteriorly).

MAXILLARY DENTITION: There are 13 (right) or 14 (left) recurved maxillary teeth, followed by two enlarged fangs lying posterior to a diastema that is about twice the length of a prediastemal socket. The fangs are deeply grooved on the anterior face nearly to the tip; the posteriormost fang is offset laterad.

HEMIPENIS: Both hemipenes were field everted; the left organ was subsequently reinflated with carmine-dyed petroleum jelly and removed for illustration (fig. 33). The left organ extended to the end of subcaudal 9, with the major retractor muscle originating at the level of subcaudal 30. The noncapitate hemipenis is bilobed, with the short lobes comprising about the distal 14 percent. The sulcus spermaticus divides basally at a point about 36 percent above the base of the organ, with the centrolineal branches terminating well short of the ends of the hemipenis, at a level proximal to the crotch of the lobes. Most of the distal 60 percent of the sulcate side of the organ is covered with calyces that are weakly papillate. The base of the organ has small spines (and spinules) extending distally

and centrifugally. These spines come to flank the asulcate side of the hemipenis, the distal 83 percent of which is depressed mediad and ornamented with large, but somewhat irregular, ill-defined "calyces." There is a small, circular depression (naked pocket) on one side of the organ at its very base.

Habitat and Natural History

The holotype of *Philodryas cordata* was found on a flat-rock outcrop at the edge of the north stream in late afternoon. This stream runs through scrubby *Stegolepis-Clusia* savanna (fig. 4). The snake was forced to disgorge a young frog of the riparian species *Leptodactylus rugosus*.

Remarks

It is worth noting that, if this snake had not been seen alive, the slight bluish color in preservative might have erroneously suggested that it could have been green in life (at least posteriorly), which is the color characteristic of the other species in the northern part of the range of *Philodryas*. Brongersma (1957) and Thomas (MS) recognized only two taxa as occurring north of the Amazon, one being *P. viridissimus* and the other a race of *P. olfersii* (including as synonym the Venezuelan *P. carbonelli* Roze fide Thomas), both of which are widespread north and south of the Amazon.

The black scale edging of *Philodryas cordata* seems only vaguely approached in a few species of Thomas' southern *borelli* group, especially *P. arnoldi* of southeastern Brazil. These species have hemipenes with spinules (as does *P. cordata*) interspersed with the spines (Thomas, MS: 242).

The hemipenis of *Philodryas cordata* does not agree well with any of the four basic types described by Thomas (MS.: 242–244), although it shares the following features with *Philodryas* generally (Thomas, MS.: 23, 38, 57, 59 [fig. 9]): The hemipenis is distally calyculate and bilobed, the sulcus spermaticus bifurcates low on the organ, a basal naked pocket is present (absent in *P. olfersi* and *P. viridissimus*, the only other species north of the Amazon), there are lateral spines in series, and there are "at least two rows of very large, shallow calyces extending down the distal one-third of the asulcate surface." The last feature is unusual among xenodontine colubrids and seems likely to be a synapomorphy of *Philodryas*.

The hemipenis of *Philodryas cordata* differs from Thomas' generic description in lacking noticeably enlarged spines (lateral spines *not* increasing distally in *cordata*) and being a heart-shaped structure with no indication of capitation. An everted hemipenis of Venezuelan *P. viridissimus* (AMNH 134204) is similar to Thomas' illustration (his fig. 9) of the everted organ of *P. nattereri* (given as representative of the "typical hemipenial morphology of *Philodryas*"), but bilobation is much less pronounced and the small calyces of the sulcate side do not extend distally over the apices onto the asulcate surfaces of the lobes (a character already noted by Thomas to differ between species). Although not strictly capitate, these organs give the appearance of having one slightly bilobed head (*P. viridissimus*) or two separate heads (*P. nattereri*), whereas the organ is not so well differentiated in *P. cordata*. One other difference between the hemipenis of *P. cordata* and those described in Thomas is probably related to the condition of eversion.[13] Everted hemipenial preparations are not available for many of the southern *Philodryas*, so it is not known whether any other species has the peculiar shape seen in *P. cordata*.

DISCUSSION

The herpetofauna of the Guayanan table mountains, which were collectively called "pantepui" by Mayr and Phelps (1967), is poorly known (for summary, see Hoogmoed, 1979). Compared with the lowlands, the summits of these physiographically diverse mesas support reduced numbers of species of

[13] Thomas (MS: 57) stated without qualification that each branch of the sulcus spermaticus extends to the lateral tip of each lobe. As emphasized elsewhere (Myers, 1974: 33), there often are topographic changes associated with hemipenial eversion, so that the apex (or apices) of the uneverted hemipenis is not necessarily the same as when the organ is everted. The points of termination of the sulcus branches are not clear in Thomas' illustration (fig. 9) of an everted hemipenis, but the branches terminate short of the tips of the everted lobes in *P. cordata* (fig. 33) and also in *P. viridissimus* (AMNH 134204).

amphibians and reptiles. It seems that amphibian and reptilian species endemic to only one or a few tepuis may be at least as commonplace as highland species that are more widely distributed.

There probably are also lowland elements at all but the highest tepui elevations. Inasmuch as the lowland distributions of Guayanan amphibians and reptiles are not well known, it usually is impossible to know if a lowland occurrence on a tepui is strictly relictual or if the species still occurs in the surrounding lowlands. A case in point is the present Guaiquinima record of *Imantodes lentiferus*, a widespread lowland species not previously recorded from Venezuela.

We were most curious to learn about the herpetofauna of the tall forest, but except for the highland *Hyla benitezi* and *Neusticurus racenisi*, only the *Imantodes* and a few other lowland species were found by extensive searches during both day and night. Anuran sounds were absent in the deep forest, which seemed ideal habitat for either low-elevation or high-elevation frogs allied to *Eleutherodactylus*—but this forest was very dry during our stay, with even the larger bromeliads lacking water, and we were aware that any number of animals *might* have been safely concealed below the second floor of the forest (see Description of Summit Camp 1).

As noted by Steyermark and Dunsterville (1980), the summit of Cerro Guaiquinima ranges in elevation from 1680 m down to 700 m, "a record low level for the summit altitudes of the major table mountains." These authors concluded that the lowland botanical influence is evidenced to a far greater extent on Cerro Guaiquinima than on the other major tepuis, and that the "typical components of the *tierra caliente* flora are co-inhabitants with the more characteristic upland flora of the tepui summit."

Although the herpetofauna is small and the flora large, the herpetological evidence is in fundamental agreement with the botanical conclusions cited above. Two-thirds of the species (10 of 15) in our sample occur commonly or largely in the *tierra caliente*, as follow:

Hyla minuta
Osteocephalus taurinus
Leptodactylus longirostris
L. rugosus
Ameiva ameiva
Anolis chrysolepis planiceps
A. fuscoauratus
Neusticurus sp., cf. *Neusticurus rudis*
Tropidurus hispidus
Imantodes lentiferus

Two additional species, a frog and lizard (*Hyla benitezi* and *Neusticurus racenisi*), occur on other tepuis and probably are best characterized as highland species—both were found in or at the edge of the tall forest. Three species that may be endemic to Guaiquinima include a lizard (*Plica lumaria*, n. sp.) and two snakes (*Liophis torrenicola*, n. sp., *Philodryas cordata*, n. sp.)—all discovered in the botanically curious *Stegolepis-Clusia* "savanna," comprising primarily tepui vegetation. These five, judged to be predominantly (if not entirely) tepui species, occurred intermixed with the greater number of lowland species.

Few additional generalizations can be made about the herpetofauna of pantepui and logical predictions may prove quite faulty. One outstanding example: Cerro Guaiquinima and a near neighbor, Auyantepui, are the only table mountains of the Roraima Formation known to harbor tropidurine lizards characterized by curious tufts of spiny neck scales—indeed, these are the only two such lizards occurring north of the Amazon. It would therefore seem reasonable to predict, as we did in the field, that the new Guaiquinima lizard is the sister species of *Tropidurus bogerti*, described by Roze (1958a) from Auyantepui. Nonetheless, although *Plica* and *Tropidurus* are part of a monophyletic group (Frost, MS), *Plica lumaria* of Guaiquinima seems much closer to the widespread lowland *P. plica* than to its tepui neighbor *T. bogerti*. Is this simply a remarkable coincidence or is it due to some biological factor (e.g., adaptive convergence to similar environments)? The question is unanswerable at this time.

Postscript

The preparation and publication of this report were among our obligations to Vene-

zuelan authorities and to the sponsor (FUDECI) of the 1990 Expedition to Cerro Guaiquinima (for other contractual obligations, see Deposition of Specimens in the introductory section of this paper). At the end of March 1991—only several weeks before going to press—we first learned of a paper by Mägdefrau et al. (1991) reporting on a collection of amphibians and reptiles from Cerro Guaiquinima; it had been published in February 1991 and marked as received at the Museum on March 6.

Although we knew that a German party had collected at several of the summit camps before us, we were not made aware of the purpose of their explorations or that they might attempt a comprehensive taxonomic treatment. We regret the duplication of effort.

Mägdefrau et al. (op. cit.) provide useful information and records for Summit Camp 2 (10 spp. at 1180 m), Camp 3 (7 spp. at 780 m elev.), Camp 4 (9 spp. at 980 m), and Camp 5 (8 spp. at 1520 m), in addition to some miscellaneous lowland records for Canaima and the Río Carapo camp.

We list below a comparison of our identifications and summit species with those in the Mägdefraus' collection (summit records extracted from Mägdefrau et al., 1991, table 2).

Given the problems of tropical herpetological collecting with limited time, the two lists are quite comparable. We include two highland species and two lowland species that they did not take. Where identifications are explicit, their list adds four widespread species to the lowland herpetofauna of Cerro Guaiquinima.

The list of Mägdefrau et al. does not add any probable endemics unless included in their unidentified material. We expected but found no evidence of *Eleutherodactylus* (see in Discussion above) and determination of their "*Eleutherodactylus* spp." will be of interest. Another *Leptodactylus* or some other leptodactylid genus would not be surprising, but the sexual or other morphs of *Leptodactylus longirostris* or *L. rugosus* could understandably lead to misassignment. We suspect that their *Philodryas* "A" and "B" represent a single brown species (*cordata*); head drawings and also color photographs are presented by Mägdefrau et al. for both specimens, but the head plate differences are the sort that appear within the normal variation of numerous colubrids.

Mägdefrau et al.	This Paper
Leptodactylus fuscus (980–1520 m)	= *Leptodactylus longirostris*
Leptodactylus rugosus (780–1520 m)	= same
Leptodactylus spp. (980–1180 m)	= morph(s) of one of above?
Eleutherodactylus spp.(780–1520 m)	= ? (not taken)
not taken	= *Hyla benitezi*
Hyla boans (780 m)	= same[14]
Hyla crepitans (980 m)	= not taken
Hyla cf. *minuta* (980–1520 m)	= *Hyla minuta*
not taken	= *Osteocephalus taurinus*
Anolis chrysolepis (980, 1520 m)	= same
not taken	= *Anolis fuscoauratus*
Plica sp. (780 m)	= *Plica lumaria*
Tropidurus torquatus (780–1180 m)	= *Tropidurus hispidus*
Ameiva ameiva (780–1180 m)	= same
not taken	= *Neusticurus racenisi*
Neusticurus rudis (1180, 1520 m)	= *Neusticurus* sp., cf. *rudis*
Leptotyphlops albifrons (1180 m)	= not taken
Chironius fuscus (1520 m)	= not taken
not taken	= *Imantodes lentiferus*
Mastigodryas b. boddaerti (780 m)	= not taken
Liophis cf. *longiventris* (1180 m)	= *Liophis torrenicola*
Philodryas sp. A (1180 m)	= *Philodryas cordata*
Philodryas sp. B (1520 m)	= *Philodryas cordata*

[14] Calling abundantly along the Río Carapo but not included in our highland list, although a single individual was taken in the south stream by Camp 1 (1030 m). It was a very emaciated adult near death. No others were found or heard and the preserved specimen was later discarded because of a strong, perhaps erroneous, suspicion that it represented an escapee transported to this camp by a previous party.

REFERENCES

Altig, Ronald, and Gail F. Johnston
1986. Major characteristics of free-living anuran tadpoles. Smithson. Herpetol. Inf. Serv. 65: 75 pp.

Beebe, William
1945. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 3. Teiidae, Amphisbaenidae and Scincidae. Zoologica 30(1): 7–32 + pls. 1–5.
1946. Field notes on the snakes of Kartabo, British Guiana, and Caripito, Venezuela. Ibid., 31(1): 11–52 + pls. 1--13.

Bokermann, Werner C. A.
1963. Girinos de anfíbios Brasileiros—I (Amphibia—Salientia). An. Acad. Bras. Cienc. 35: 465–474.
1967. Notas sôbre cantos nupciais de anfíbios Brasileiros (Anura). III. Ibid., 39(3/4): 491–493 + pl.

Boulenger, George Albert
1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum. London: British Museum, xvi + 503 pp. + 30 pl.
1896. Catalogue of the snakes in the British Museum (Natural History). Vol. 3. London: British Museum (Natural History), xiv + 727 pp. + 25 pls.
1900. Reptiles and Batrachians. *In* E. R. Lankester, Report on a collection made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. Reptiles. Trans. Linnean Soc. London, Zool., ser. 2, 8(2): 53–56 + pl. 5.

Brongersma, L. D.
1957. On two species of the genus Philodryas (Serpentes) from Surinam. Proc. K. Nederl. Akad. Wet. (Amsterdam), ser. C, 60(4): 458–462.

Burt, Charles E., and May Danheim Burt
1931. South American lizards in the collection of the American Museum of Natural History. Bull. Am. Mus. Nat. Hist. 61: 227–395.

Cardoso, Ado José
MS. Organizaço espacial e temporal na reproduço e vida larvária em uma comunidade de hilídeos no sudeste do Brasil. Unpubl. diss., Instit. Biologia Univ. Estadual de Campinas, Brazil, [iv] + 106 pp.

Cardoso, Ado José, and Célio F. B. Haddad
1984. Variabilidade acústic em diferentes populaçes e interaçes agressivas de *Hyla minuta* (Amphibia, Anura). Ciência e Cultura 36(8): 1393–1400.

Cei, José M.
1980. Amphibians of Argentina. Monitore Zool. Italiano 2: 1--609.

Cochran, Doris M.
1955. Frogs of southeastern Brazil. U.S. Nat. Hist. Mus. Bull. 206: 1–423.

Cochran, Doris M., and Coleman J. Goin
1970. The frogs of Colombia. Ibid., 288: 1–655.

Cope, Edward Drinker
1894. On the species of *Himantodes* D & B. Am. Nat. 28: 612—615.

d'Orbigny, Alcide
1837. L'Anolis Brundoré. *In* A. M. C. Duméril and G. Bibron, Erpétologie général ou histoire naturelle complète des reptiles, 4: 110-111. Paris: Librairie Encyclopédique de Roret (1834–1854).

Dixon, James R.
1983. The *Liophis cobella* group of the Neotropical colubrid snake genus *Liophis*. J. Herpetol. 17: 149–165.

Dixon James R., and William W. Lamar
1981. A new species of microteiid lizard (Genus *Neusticurus*) from Colombia. J. Herpetol. 15: 309–314.

Donnelly, Maureen A., Craig Guyer, and Rafael O. de Sá
1990. The tadpole of a dart-poison frog *Phyllobates lugubris* (Anura: Dendrobatidae). Proc. Biol. Soc. Washington 103: 427–431.

Duellman, William E.
1969. A new species of frog in the *Hyla parviceps* group. Herpetologica 25: 241–247.
1974. A reassessment of the taxonomic status of some Neotropical hylid frogs. Occas. Paps. Mus. Nat. Hist. Univ. Kansas 27: 1–27.
1977. Liste der rezenten Amphibian und Reptilien Hylidae, Centrolenidae, Pseudidae. Das Tierreich 95: 1–225.
1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 65: 1–352.
1982. A new species of small yellow *Hyla* from Peru (Anura: Hylidae). Amphibia-Reptilia 3: 151–160.

Duellman, William E., and M. J. Fouquette, Jr.
1968. Middle American frogs of the *Hyla microcephala* group. Univ. Kansas Publ. Mus. Nat. Hist. 17: 517–557.

Duellman, William E., and Linda Trueb
1983. Frogs of the *Hyla columbiana* group: taxonomy and phylogenetic relation-

ships. *In* G. Anders et al. (eds.), Advances in Herpetology and Evolutionary Biology. Cambridge, MA: Museum of Comparative Zoology, pp. 33–51.

Echternacht, Arthur C.
1971. Middle American lizards of the genus *Ameiva* (Teiidae) with emphasis on geographic variation. Misc. Publ. Univ. Kansas Mus. Nat. Hist. 55: 86 pp.

Etheridge, Richard
1970. A review of the South American iguanid lizard genus *Plica*. Bull. British Mus. (Nat. Hist.), Zool., 19(7): 235–256.

Etheridge, Richard, and Kevin de Queiroz
1988. A phylogeny of Iguanidae. *In* Richard Estes and Gregory Pregill (eds.), Phylogenetic relationships of lizard families: essays commemorating Charles L. Camp. Stanford: Stanford Univ. Press, pp. 283–368.

Frost, Darrel R.
1985. (ed.) Amphibian species of the world. Lawrence, KS: Allen Press and Assoc. Syst. Coll., vii + 732 pp.
MS. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Tropiduridae: Tropidurinae).

Frost, Darrel R., and Richard Etheridge
1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Misc. Publ. Univ. Kansas Mus. Nat. Hist. 81: 1–65.

Gosner, Kenneth L.
1960. A simplified table for staging anurans embryos and larvae with notes on identification. Herpetologica 16: 183–190

Heatwole, Harold, Haydee Solano, and Audry Heatwole
1965. Notes on amphibians from the Venezuelan Guyanas with description of two new forms. Acta Biol. Venezuelica 4: 349–364.

Heyer, W. Ronald
1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Nat. Hist. Mus. Los Angeles Co. Sci. Bull. 29: 1–85.
1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). Smithson. Contrib. Zool. 301: 1–43.

Hoogmoed, Marinus S.
1973. Notes on the herpetofauna of Surinam IV. The lizards and amphisbaenians of Surinam. Biogeographica 4: 1—419.
1979. The herpetofauna of the Guianan region. *In* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution, and dispersal. Monogr. Mus. Nat. Hist. Univ. Kansas 7: 241–279.

Hoogmoed, Marinus S., and Ulrich Gruber
1983. Spix and Wagler type specimens of reptiles and amphibians in the Natural History Musea in Munich (Germany) and Leiden (The Netherlands). Spixiana, suppl. 9: 319–415.

Kenny, Julian S.
1969. The Amphibia of Trinidad. Stud. Fauna Curaçao Carib. Is. 29: 1–78

Lavilla, Esteban O.
1990. The tadpole of *Hyla nana* (Anura: Hylidae). J. Herpetol. 24: 207–209.

Linnaeus, Carolus
1758. Systema Naturae. 10 ed., vol. 1: [iv] + 824 pp., Stockholm.

Lutz, Bertha
1973. Brazilian species of *Hyla*. Austin, TX: Univ. Texas Press, 260 pp.

Mägdefrau, Helmut, Karin Mägdefrau, and Andreas Schlüter
1991. Herpetologische Daten vom Guaiquinima-Tepui, Venezuela. Herpetofauna (Germany), 13(70): 13–26.

Mayr, Ernst, and William H. Phelps, Jr.
1967. The origin of the bird fauna of the South Venezuelan highlands. Bull. Am. Mus. Nat. Hist. 136: 273–327 + pls. 14–21.

Myers, Charles W.
1969. The ecological geography of cloud forest in Panama. Am. Mus. Novitates 2396: 52 pp.
1974. The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. Bull. Am. Mus. Nat. Hist. 153(1): 262 pp.
1982. Blunt-headed vine snakes (*Imantodes*) in Panama, including a new species and other revisionary notes. Am. Mus. Novitates 2738: 50 pp.

Noble, G. Kingsley
1923. New batrachians from the Tropical Research Station British Guiana. Zoologica 3(14): 289–299.

Peters, James A., and Roberto Donoso-Barros
1970. Catalogue of the Neotropical squamata. Part II. Lizards and amphisbaenians. Washington, D.C.: Smithsonian Inst. Press, 293 pp.

Peters, James A., and Braulio Orejas-Miranda
1970. Catalogue of the Neotropical squamata. Part I. Snakes. Washington, D.C.: Smithsonian Inst. Press, 347 pp.

Peters, Wilhelm
1872. Mittheilung über eine Sammlung von Batrachiern aus Neu-Freiburg in Bras-

ilien. Monatsber. K. Preussichen Akad. Wiss. Berlin, for 1872: 680–684.

Rivero, Juan A.
1961. Salientia of Venezuela. Bull. Mus. Comp. Zool. 126: 207 pp.
"1967" [1968]. Anfibios coleccionados por la Expedición Franco-Venezolana al Alto Orinoco 1951–1952. Carribean J. Sci. 7(3–4): 145–154.
1969. On the identity and relationships of *Hyla luteocellata* Roux (Amphibia, Salientia). Herpetologica 25(2): 126—134.
1971. Tres nuevos records y una nueva especie de anfibios de Venezuela. Carribean J. Sci. 11(1–2): 1–9.
"1971" [1972]. Notas sobre los anfibios de Venezuela. I. Sobre los hilidos de la Guayana Venezolana. Ibid. 11 (3–4): 181–193.

Rivero, Juan A., and Andrés Eloy Esteves
1969. Observations on the agonistic and breeding behavior of *Leptodactylus pentadactylus* and other amphibian species in Venezuela. Breviora 321: 14 pp.

Rodrigues, Miguel Trefaut
1987. Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao sul do Rio Amazonas (Sauria, Iguanidae). Arq. Zool., São Paulo 31: 105–230.

Roze, J. A.
1958a. Los reptiles del Auyantepui, Venezuela, basándose en las colecciones de las expediciones de Phelps-Tate, del American Museum of Natural History, 1937-1938, y de la Universidad Central de Venezuela, 1956. Acta Biol. Venezuelica 2(22): 243–270.
1958b. Los reptiles del Chimantá Tepui (Estado Bolívar, Venezuela) colectados por la expedición botánica del Chicago Natural History Museum. Ibid., 2(25): 299–314.
1966. La taxonomia y zoogeografía de los ofidios en Venezuela. Caracas: Univ. Central Venezuela, 362 pp.

Spix, Joannes Bapt. de
1825. Animalia nova sive species novae lacertarum, quas in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae Regis suscepto collegit et descripsit Dr. J. B. de Spix. Munich, Hübschmann, 26 pp. + 30 pls. [pls. I–XXVIIIi + XIII[a], xiv[a]].

Steindachner, Franz
1862. Über zwei noch unbeschriebene Batrachier aus den Sammlungen des K. K. Zoologischen Museum in Wien. Arch. Zool. Anat. Fisiol. (Genova) 2(1): 77–82 + pl. 6.

Steyermark, Julian A., and G. C. K. Dunsterville
1980. The lowland floral element on the summit of Cerro Guaiquinima and other cerros of the Guayana highland of Venezuela. J. Biogeogr. 7: 285–303.

Thibaudeau, D. Giselle, and Ronald Altig
1988. Sequence of ontogenetic development and atrophy of the oral apparatus of six anuran tadpoles. J. Morphol. 197: 63–69.

Thomas, Robert Allen
MS. A revision of the South American colubrid snake genus *Philodryas* Wagler, 1830. Unpubl. Ph.D. diss. Texas A&M Univ., xiv + 324 pp. (1976). [Diss. Abst. Internatl. B, 37(8): 3815-B, 1977]

Troschel, F. H.
1848. Amphibien. *In* R. Schomburgk, Reisen in Britisch-Guiana in den Jahren 1840–1844, Theil 3, Versuch einer Fauna und Flora von Britisch-Guiana, pp. 645–661. Leipzig: Verlagsbuchhandlung von J. J. Weber.

Trueb, Linda, and William E. Duellman
1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 1: 47 pp.

Uzzell, Thomas M., Jr.
1966. Teiid lizards of the genus *Neusticurus* (Reptilia, Sauria). Bull. Am. Mus. Nat. Hist. 132(5): 277–327.

Van Devender, Robert Wayne
1969. Resurrection of *Neusticurus racenisi* (Sauria, Teiidae). J. Herpetol. 3(1–2): 105–107.

Vanzolini, P. E., and Ernest E. Williams
1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. São Paulo 19: 1–298.

Vizotto, Luiz Dino
1967. Desenvolvimento de anuros da regio norte-ocidental do Estado de São Paulo. Rec. Fac. Filos. Cienc. Letr. S. J. Rio Preto Zool. Especial, 161 pp.

Wagler, Joh. [Joannes Georg]
1830. Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel. Munich, Stuttgart and Tübingen, J. G. Cotta, vi + 354 pp.

Zimmer, John T., and William H. Phelps
1946. Twenty-three new subspecies of birds from Venezuela and Brazil. Am. Mus. Novitates 1312: 23 pp.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates, Bulletin,* and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.